STRATIGRAPHIC DISTRIBUTION OF BRACHIOPODS

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INTRODUCTION

The compilation of the revised brachiopod *Treatise* presented an outstanding opportunity for a detailed investigation of the stratigraphic distribution of the phylum. This comprehensive taxonomic census has produced a prodigious amount of information on the occurrences of brachiopod genera, on all continents and all Phanerozoic stratigraphic horizons, with a precision that has never before been achieved. The records available are not perfect, but they are as close to perfect as can be achieved given the vagaries of preservation in the geologic record and the many other complications that affect the reliability of stratigraphic data.

This chapter presents a brief synthesis of the accumulated data on the stratigraphic distribution of the entire phylum, covering the stratigraphic distributions of a total of over 4200 genera. The data are presented by system and are summarized by order, and hence this chapter only skims the surface of the available information that covers all constituent taxonomic levels from genera upward, and at a resolution of individual stages. This chapter describes the distribution of orders and makes brief reference to the wider biological and geologic implications of major features of these distributions, but space precludes detailed discussion. The analysis presented here includes the most up-to-date stratigraphic information available, including the stratigraphic distributions of recently described genera (herein, p. 2532–2821), as well as any new updated stratigraphic information on genera published in earlier volumes (in effect all available, valid, stratigraphic information on brachiopods up to mid-September 2006).

STRATIGRAPHIC NOMENCLATURE

The aim of this chapter is to analyze the distribution of brachiopods in terms of standardized stratigraphic units. All the data used here comes directly from the generic records in the *Treatise* volumes 2 to 6 (2000–2007). Of overriding importance for the stratigraphic analyses presented here was the decision taken at the outset of the project to adopt a single stratigraphic scale for all *Treatise* descriptions. Such a decision was agreed by all authors, at the instigation of Coordinating Author Alwyn Williams, and thereby provided a standardized stratigraphic classification for all taxonomic descriptions. Our knowledge of global stratigraphy is changing fast, and over the last 16 years as this *Treatise* revision was being prepared, there have been major emendations to the naming, correlation, and absolute dating of stratigraphic units. While such changes are valuable in advancing the resolution and accuracy of stratigraphic analysis, they are problematic for a *Treatise* compilation. To have attempted to keep in step with such changes over a 16-year period would have created a totally confusing situation in which it was impossible to know how to compare stratigraphic data compiled by different researchers.

In addition, books such as this have a long shelf life, almost 40 years in the case of the original brachiopod *Treatise* (MOORE, 1965), and hence the data presented must be standardized throughout the entire series of volumes to avoid present and future confusion, as far as is possible. For this reason, all authors for the revisions of the brachiopod *Treatise* agreed to use the stratigraphic chart published by the International Union of Geological Sciences (IUGS) in 1989 (Cowie & Bassett, 1989). An abbreviated version of the standard stratigraphic scale has been included in the preface of every volume of the revised brachiopod *Treatise* (e.g., p. xx in Vol. 1 [Kaesler, 1998], or herein, p. xxix) listing a total of 38 series assigned to 12 different systems. Many taxonomic descriptions in the *Treatise* do indeed cite stratigraphic ranges down to stage level. It was also invaluable to have a comprehensive taxonomic framework for the entire phylum established in advance of starting the compilation of the stratigraphic data in the form of a supraordinal classification (Williams & others, 1996).

It is important to clarify some aspects of the complex and potentially confusing protocols of stratigraphic nomenclature. Historically, subdivisions of the stratigraphic scale, such as stage, were defined by stratotypes, based on a combination of localized lithologic units and major evolutionary events, such as extinctions or radiations. These stages were readily applicable within a restricted geographic area but were much more problematic in attempts to apply them globally because of correlation complications and the existence of many discontinuities in the geologic record. As a result, discrete geographic regions and countries often adopted quite different stratigraphic classifications, based on different and nonoverlapping nomenclatures. Thus, the 1982 compilation of *A Geologic Time Scale* (Harland & others, 1982) had to correlate a number of quite different regional stratigraphic classifications in an attempt to establish a globally applicable scheme. For example, the Cretaceous chart had to reconcile a total of seven entirely different stage nomenclatures, from France, England, the USSR, Japan, New Zealand, Canada, and the United States (Harland & others, 1982).

Stratigraphic procedures are further complicated by the understandable interest in the integration of absolute time determinations (such as are available from radiometric dating of rocks) into the stratigraphic framework. This led to a modification of the concepts of stratigraphic classification, with terms such as system, series, and stage being considered as chronostratigraphic (or time-rock) units, each consisting of all the rocks formed globally during a specified time interval (Gradstein, Ogg, & Smith, 2004). However, the establishment of a fully functional geologic time scale requires that the chronostratigraphic scale be calibrated using a chronometric scale of absolute dates (Gradstein, Ogg, & Smith, 2004). Merging of the two scales was complicated by the fact that the physical geologic record is punctuated by gaps, in contrast to abstract geologic time, which is continuous (Gradstein, Ogg, & Smith, 2004). The disparity between these two scales became so acute as the precision and scope of absolute dating increased that it was necessary to develop a distinct but parallel chronometric nomenclature to distinguish between absolute time on one hand and chronostratigraphic units on the other. In the chronometric scale, terms such as period, epoch, and age were the direct equivalent of system, series, and stage as used in chronostratigraphy. Strictly speaking, therefore, the term Permian Period refers to a range of absolute time expressed in millions of years, while the term Permian System refers to all the rock that accumulated during that particular time.

In practice, however, the terms system and period are often used interchangeably. This dual nomenclature is clearly less than ideal, and recent efforts have concentrated on defining Global Stratotype Sections and Points (GSSPs) that mark the beginning of chronostratigraphic units with precisely defined, globally applicable, isochronous horizons, in many respects rendering the dual system obsolete and unnecessary (Walsh, 2001, 2003; Remane, 2003). GSSPs are not yet available for all subdivisions of geologic time, however. Accordingly chronostratigraphic units, as portrayed in the 1989 IUGS Chart and used throughout the *Treatise* revision, will also be used in this chapter. In any meaningful sense, terms such as system and stage are directly equivalent to period and age respectively in the geochronologic scale. Most diagrams plotted here use the chronostratigraphic units as the horizontal ordinate, with each stage equally spaced, and hence make no attempt to account for differences in absolute time duration of individual stages.

STRATIGRAPHIC SUBDIVISIONS

The major increase in resolution of the resulting stratigraphic analysis reported herein, as compared with the previous *Treatise*, is readily apparent. In 1965, the entire geologic history of the brachiopods was summarized in graphs with a maximum of 28 census points, mostly corresponding to lower, middle, and upper divisions of individual systems (e.g., Lower Ordovician, Upper Permian). By contrast, the analyses presented here divide the geologic history of the brachiopods into 113 census points, overwhelmingly corresponding to named stages in the 1989 IUGS chart.

Arriving at these 113 units was not just a matter of extracting the appropriate names from the IUGS chart, however. In 1989, as with all compilations of stratigraphic units, there were some systems that were clearly subdivided with names that were universally or widely accepted, while there were others for which contrasting nomenclatures were in usage, often varying in different countries with no international agreements or correlations. Such complexities will probably always bedevil stratigraphic analysis and reanalysis, but for this compilation the 113-point census scale was developed before any of the taxonomic descriptions became available, and having been agreed in advance by the *Treatise* authors, it is therefore consistent for all taxa analyzed in this chapter (Table 40, and see discussion below).

Even with this prior agreement, plotting cited stratigraphic distributions is not always straightforward. An encouraging number of stratigraphic distributions in this *Treatise* were cited using the stages defined in the 1989 IUGS compilation, implying a high degree of resolution of our existing knowledge of the taxon's geologic history. For others, the citation of a stratigraphic range in terms of an entire system or systems is open to numerous interpretations and at least implies lower stratigraphic resolution. Thus, the citation of Ordovician could indicate the taxon is known to be present in all stages of the Ordovician (and hence its range is known very accurately), or at the other extreme its range could be poorly known although definitely recorded from some subdivision or subdivisions of the Ordovician. Or it could indicate that it is found in rocks that are definitely known to be Ordovician, but its precise range cannot be more accurately determined from the original published descriptions. Such a citation could also mean that the genus is poorly constrained in terms of its stratigraphic range but is assumed, suspected, or inferred by the compiling author to be present in Ordovician rocks.

All that can be done in these cases is to adopt a standard protocol, and in keeping with the practice adopted in the previous brachiopod *Treatise* (WILLIAMS, 1965b), citations of a system has been interpreted as being present in all stages of that system (the so-called range-through assumption). Undoubtedly this will overestimate the stratigraphic range of some taxa, but as long as that is clearly realized by all users of the *Treatise* as being the inevitable consequences of how stratigraphic data are recorded, there will be no significant problems.

Furthermore, for some systems, such as the Permian and Carboniferous, there were several different stratigraphic schemes in common use during the compilation of the *Treatise* data, and these were used by *Treatise* authors who often had no alternative but to cite records using the scheme prevalent in the geographic area from where the fossils were collected and described. Similar and inevitable problems occur when the only stratigraphic information available to the

Table 40. Overview of stratigraphic zonation scheme used for all analyses in this chapter, based largely on 1989 IUGS chart (Cowie & Bassett, 1989). Conventions used to interpret cited ranges from *Treatise* descriptions that are not present in IUGS chart are also included (i.e., use of Lopingian for Upper Permian). Names enclosed in "…" are not formal stratigraphic names but are used throughout as convenient, widely recognized labels (for example, for stages that have not been formally defined and named). Some of the names included under the series heading (column 2) are similarly not formalized, and many include part stages but are again included as commonly used terms in stratigraphic determinations. Individual stage names are listed as are the standardized three letter codes for each stage (e.g., TOM for Tommotian). Columns 5, 6, and 7 list absolute age determinations for midstage, base, and duration in millions of years of each stage. Graphs in this chapter plotted using absolute age ordinates use midstage age. Absolute age data are cited in millions of years before present (i.e., Ma) for base and midpoint of each stage; they are an amalgamation of dates from 1989 IUGS chart and widely accepted absolute dating modifications current during 1999. Dates presented in this table therefore correspond to no single compilation of the Geological Time Scale (Gradstein, Ogg, & Smith, 2004) (new).

System	Series	Stage	Code	Midstage Age	Base (Ma)	Duration (myr)	Stage No.
"Quaternary"	"Holocene"	"Holocene"	HOL	0.0	0.0		1
	"Pleistocene"	"Pleistocene"	PLE	0.8	1.6	1.6	2
Neogene	Pliocene	Piacenzian	PIA	2.5	3.3	1.7	3
		Zanclean	ZAN	4.2	5.1	1.8	4
	Miocene	Messinian	MES	5.8	6.5	1.4	5
		Tortonian	TOR	8.9	11.3	4.8	6
		Serravallian	SRV	13.2	15.0	3.7	7
		Langhian	LAN	15.6	16.2	1.2	8
		Burdigalian	BUR	17.6	19.0	2.8	9
		Aquitanian	AQT	21.0	23.0	4.0	10
Paleogene	Oligocene	Chattian	CHT	25.0	27.0	4.0	11
		Rupelian	RUP	28.8	30.5	3.5	12
	Eocene	Priabonian	PRB	32.3	34.0	3.5	13
		Bartonian	BRT	36.5	39.0	5.0	14
		Lutetian	LUT	42.0	45.0	6.0	15
		Ypresian	YPR	49.0	53.0	8.0	16
	Paleocene	Thanetian	THA	56.0	59.0	6.0	17
		Danian	DAN	61.7	64.4	5.4	18
Cretaceous	Upper Cretaceous	Maastrichtian	MAA	64.5	64.6	0.2	19
		Campanian	CMP	73.8	83.0	18.4	20
		Santonian	SAN	84.5	86.0	3.0	21
		Coniacian	CON	87.0	88.0	2.0	22
		Turonian	TUR	89.5	91.0	3.0	23
		Cenomanian	CEN	93.0	95.0	4.0	24
	Lower Cretaceous	Albian	ALB	101.0	107.0	12.0	25
		Aptian	APT	110.5	114.0	7.0	26
		Barremian	BRM	115.0	116.0	2.0	27
		Hauterivian	HAU	118.0	120.0	4.0	28
		Valanginian	VLG	124.0	128.0	8.0	29
		Berriasian	BER	131.5	135.0	7.0	30
Jurassic	Upper Jurassic	Tithonian	TTH	137.0	139.0	4.0	31
		Kimmeridgian	KIM	141.5	144.0	5.0	32
		Oxfordian	OXF	148.0	152.0	8.0	33
	Middle Jurassic	Callovian	CLV	155.5	159.0	7.0	34
		Bathonian	BTH	164.5	170.0	11.0	35
		Bajocian	BAJ	173.0	176.0	6.0	36
		Aalenian	AAL	178.0	180.0	4.0	37
	Lower Jurassic	Toarcian	TOA	184.0	188.0	8.0	38

Table 40. *Continued.*

		Pliensbachian	PLB	191.5	195.0	7.0	39
		Sinemurian	SIN	198.0	201.0	6.0	40
		Hettangian	HET	203.0	205.0	4.0	41
Triassic	Upper Triassic	Rhaetian	RHT	207.5	210.0	5.0	42
		Norian	NOR	215.0	220.0	10.0	43
		Carnian	CRN	225.0	230.0	10.0	44
	Middle Triassic	Ladinian	LAD	232.5	235.0	5.0	45
		Anisian	ANS	237.5	240.0	5.0	46
	Lower Triassic	Scythian	SCY	245.0	250.0	10.0	47
Permian	Upper Permian	Changhsingian	CHA	252.5	255.0	5.0	48
		Capitanian	CAP	256.3	257.5	2.5	49
		Wordian	WOR	258.8	260.0	2.5	50
	Lower Permian	Roadian	ROA	265.0	270.0	10.0	51
		Artinskian	ART	272.5	275.0	5.0	52
		Sakmarian	SAK	277.5	280.0	5.0	53
		Asselian	ASS	285.0	290.0	10.0	54
Carboniferous	“Upper Gzhelian”	“Upper Gzhelian”	GZE	291.7	293.3	3.3	55
	Kasimovian	Barruelian	BAR	295.0	296.7	3.4	56
		Cantabrian	CAN	298.4	300.0	3.3	57
	“Westphalian D”	“Westphalian D”	WES	301.3	302.5	2.5	58
	Moscovian	Bolsovian	BOL	303.8	305.0	2.5	59
		Duckmantian	DUC	306.3	307.5	2.5	60
	Bashkirian	Langsettian	LAN	308.8	310.0	2.5	61
		Yeadonian	YEA	311.1	312.1	2.1	62
		Marsdenian	MAR	313.2	314.3	2.1	63
		Kinderscoutian	KIN	315.3	316.4	2.1	64
	Serpukhovian	Alportian	ALP	317.4	318.5	2.1	65
		Chokierian	CHO	319.6	320.6	2.1	66
		Arnsbergian	ARN	321.7	322.8	2.1	67
		Pendleian	PEN	323.9	325.0	2.3	68
	Viséan	Brigantian	BRI	327.1	329.3	4.3	69
		Asbian	ASB	331.4	333.6	4.3	70
		Holkerian	HOL	335.7	337.9	4.3	71
		Arundian	SPK	340.0	342.1	4.3	72
		Chadian	VIS	344.3	346.4	4.3	73
	Tournaisian	Ivorian	IVO	348.6	350.7	4.3	74
		Hastarian	HAS	352.9	355.0	4.3	75
Devonian	Upper Devonian	Famennian	FAM	360.0	365.0	10.0	76
		Frasnian	FRS	370.0	375.0	10.0	77
	Middle Devonian	Givetian	GIV	377.5	380.0	5.0	78
		Eifelian	EIF	382.5	385.0	5.0	79
	Lower Devonian	Emsian	EMS	387.5	390.0	5.0	80
		Pragian	PRA	395.0	400.0	10.0	81
		Lochkovian	LOC	405.0	410.0	10.0	82
Silurian	“Přídolí”	“Přídolí”	PRD	412.3	414.7	4.7	83
	Ludlow	Ludfordian	LUD	417.0	419.3	4.7	84
		Gorstian	GOR	421.7	424.0	4.7	85
	Wenlock	Homerian	HOM	425.0	426.0	2.0	86
		Sheinwoodian	SHE	427.0	428.0	2.0	87
	Llandovery	Telychian	TEL	429.7	431.3	3.3	88
		Aeronian	AER	433.0	434.7	3.3	89
		Rhuddanian	RHU	436.3	438.0	3.3	90
Ordovician	Cincinnatian	Hirnantian	HIR	439.0	440.0	2.0	91
		Rawtheyan	RAW	441.0	442.0	2.0	92
		Cautleyan	CAU	443.0	444.0	2.0	93
		Pusgillian	PUS	445.0	446.0	2.0	94
		Onnian	ONN	446.6	447.3	1.3	95
		Actonian	ACT	447.9	448.6	1.3	96

Table 40. *Continued.*

	Champlainian	Marshbrookian	MAR	449.2	449.9	1.3	97
		Longvillian	LON	450.5	451.1	1.3	98
		Soudleyan	SOU	451.8	452.4	1.3	99
		Harnagian	HAR	453.1	453.7	1.3	100
		Costonian	COS	454.4	455.0	1.3	101
		"Llandeilo-Llanvirn"	LLL	462.5	470.0	15.0	102
		"Arenig"	ARG	476.5	483.0	13.0	103
	Canadian (incl. lower Arenig)	"Tremadoc"	TRE	486.5	490.0	7.0	104
Cambrian	Upper Cambrian	Trempealeauan	TRM	491.7	493.3	3.3	105
		Franconian	FRA	495.0	496.7	3.3	106
		Dresbachian	DRE	498.3	500.0	3.3	107
	Middle Cambrian	Mayaian	MAY	502.3	504.5	4.5	108
		Amgaian	AMG	506.8	509.0	4.5	109
	Lower Cambrian	Toyonian	TOY	514.3	519.5	10.5	110
		Botomian	BOT	524.8	530.0	10.5	111
		Atdabanian	ATD	532.5	535.0	5.0	112
		Tommotian	TOM	537.5	540.0	5.0	113

Treatise researchers were published records from the past, which used outdated stratigraphic nomenclature. Again, standard protocols have been adopted for dealing with all such cases; not everyone will necessarily agree with such conventions, but they are at least applied consistently throughout this chapter.

Another important convention adopted throughout this stratigraphic analysis was the method of handling question marks (?) to indicate either doubtful taxa or doubtful stratigraphic ranges. Before starting this analysis, the authors of this chapter (including the late Alwyn Williams) agreed that all records marked with a question mark were to be excluded, because such records indicated that the compiling authors had significant reservations about the validity of these records. Furthermore, any component of the cited stratigraphic record of a genus that included a question mark was also excluded. Thus, in a record that read "Antarctica, ?Upper Cretaceous, Paleogene–Holocene," the taxon would only be recorded as being present from the Paleogene to the Holocene and not in the Cretaceous. Again there was considerable value in applying this convention consistently to all the stratigraphic ranges cited in the new *Treatise*, as it will widen the application and maximize the shelf life of this volume. As the main focus of this chapter is to analyze the stratigraphic distribution of brachiopod orders, valid genera listed within the *Treatise* that were not assigned to one of the 26 established orders (i.e., listed as order Uncertain) were also excluded from this stratigraphic analysis. As the number of genera in this category was very small, the effect of such a procedure on the overall distribution of the brachiopods is insignificant.

ABSOLUTE GEOLOGIC TIME

As discussed above, it is desirable to assign absolute ages to stratigraphic units, and thereby present the data using a time rather than a stratigraphic scale. The absolute dating of stratigraphic units has also changed markedly over recent years, however, arguably more radically than the stratigraphic units themselves. The most recent version of *A Geologic Time Scale 2004* (Gradstein, Ogg, & Smith, 2004) used figures to display just how profoundly the absolute time scale had changed over the last 50 years or so (Gradstein, Ogg, & Smith, 2004, fig. 1.5–1.6). These graphs compared the geologic time scales as presented by Arthur Holmes in 1937, with the latest version compiled by Gradstein, Ogg, and Smith (2004). In the modern synthesis, the Ordovician, Silurian, Devonian, Carboniferous, Permian, Triassic, and Jurassic are assigned ages that are entirely different and nonoverlapping with those cited by Holmes, while there are significant areas of nonoverlap in ages assigned to the Cambrian and Cretaceous. In effect, therefore, the absolute geologic time scale has changed completely over the last 67 years, and there is every likelihood that it will continue to evolve incrementally over the coming decades. This results from different absolute ages for the starts and ends of geologic systems, as well as significant changes in the duration of some individual systems and stages.

Indeed, by the time work started on this chapter in 1999, there were already some significant absolute age changes that had become widely accepted from the dates presented in the IUGS 1989 stratigraphic chart (Cowie & Bassett, 1989). For example, the base of the Cambrian System, cited at around 570 Ma (with alternative sources giving 540) in the 1989 IUGS Chart was, by 1999, widely recognized as much more accurately considered as 540 Ma (and 542 Ma in Gradstein, Ogg, & Smith, 2004). Similar adjustments were required to the absolute ages assigned to the base of the Ordovician System, from 510 Ma cited in the 1989 IUGS Chart to 490 Ma in more recent compilations. In view of the long shelf life of the *Treatise*, it was clearly inappropriate to use an absolute time scale when presenting the stratigraphic data, as the raw data had not been compiled as absolute ages and as it is very likely that the absolute time scale will continue to evolve. So using absolute age dates throughout would give primacy to what is essentially secondary information derived from the stratigraphic information, as opposed to data collected in terms of a standardized scheme of chronostratigraphic units. As Alwyn Williams, one of the original authors of this chapter, wrote in 1999:

"We are constrained by two considerations:

* The chapter is about the 'stratigraphic distribution' of brachiopods;

* The decision taken in 1990 to standardize all our stratigraphic terminology in line with that of the IUGS chart.

These constraints immediately relegate absolute time ordinates to derived text figures. In the first instance, all our processed data should be presented according to the chronostratigraphic units set out in the IUGS chart."

Absolute time plots, however, do have some significant advantages over stratigraphic plots, most notably in providing a more realistic portrayal of the rate of changes. In this chapter a few graphs using absolute age ordinates are presented where such a procedure contributes significantly to the discussion. Wherever this has been done, a different, simplified, graphical format has been adopted to emphasize the derived nature of the graph. Such an approach, for example, has been used to demonstrate the major biodiversification event at the beginning of the Ordovician (see Fig. 1914 and 1919). When plotted using chronostratigraphic ordinates, this appears to be a very rapid event, but plotted using time ordinates it becomes a much more gradual event (for example, see the comparison between Fig. 1912 and 1914 below).

Because of the evolving establishment of a chronometric scale for Earth history since 1989 it is important for us to be explicit in stating the absolute ages used in any analysis presented here. Thus, Table 40 represents a composite of the dates given in the 1989 IUGS chart, together with the widely accepted modifications up to 1999 (when the stratigraphic analysis of brachiopod taxa began). Absolute age determinations, in millions of years, were assigned to each of the 113 subdivisions of the Phanerozoic (predominantly corresponding to stages) used in the analysis (Table 40). Major boundaries, such as those between systems, were generally well constrained in absolute terms, but ages for some stages had to be extrapolated using the nearest dated horizons. These absolute dates were then frozen at their 1999 state, again to avoid future confusion. If major changes to absolute age determinations have appeared in more recent work (for example, Gradstein, Ogg, &

SMITH, 2004), these are discussed in the text, but have not been included in Table 40. The absolute ages from the most recent compilation of the geologic time scale (GRADSTEIN, OGG, & SMITH, 2004), however, have been cited at the beginning of each section dealing with the stratigraphic distribution of brachiopods within a system. Although potentially confusing, this practice simply recognizes the dynamic nature of stratigraphic procedures and dating; as the source of the differing dates are fully acknowledged in each case, this chapter reflects the significant changes that have taken place in the absolute dating of systems from the 1989 IUGS chart to the 2004 geologic time scale compilation (GRADSTEIN, OGG, & SMITH, 2004).

The absolute dates used result in a mean duration for each stage of 4.8 million years (standard deviation = 3.3 million years). The stages range in duration from 18.4 million years to 0.2 million years (excluding the Holocene, which is essentially used to describe Recent, or living taxa, but has a nominal duration of 10,000 years). There are notable variations in the durations of stages within different systems, which clearly have an influence on the distributional patterns. For example, the Carboniferous System is divided into a large number of stages that are of relatively similar duration (21 stages, with a mean duration of 3.1 million years (standard deviation = 0.9 million years). By comparison, the mean duration of Ordovician stages is very similar (3.7 million years), but the standard deviation is much higher (4.6 million years). This discrepancy is a reflection of much greater variation in the duration of the individual stages, with the Lower Ordovician stages being of much longer duration (Tremadoc: 7.0 million years; Arenig: 13.0 million years; Llandeilo-Llanvirn: 15.0 million years). The mean duration of Upper Ordovician stages is much less (at 1.5 ± 0.4 million years). Similar heterogeneities are apparent at other parts of the stratigraphic column. The stage with the longest duration is the Campanian of the Upper Cretaceous, while the average duration of the Lower Cretaceous is similarly distorted by the abnormally long Albian Stage (12 million years). In the Upper Cretaceous the longest stage (Campanian) is immediately followed by the shortest (Maastrichtian). Such inconsistencies are being addressed in the latest version of the geologic time scales but are not yet fully in place (for example, the Ordovician includes 7 (rather than 14) stages of more homogeneous duration, but 4 of them are as yet unnamed; GRADSTEIN, OGG, & SMITH, 2004). A more refined subdivision of the Ordovician into 19 time slices was described by WEBBY, COOPER, and others (2004) and used as the basis for stratigraphic analysis conducted on the Great Ordovician Biodiversification Event (WEBBY, PARIS, & others, 2004).

METHODOLOGY

In this chapter the emphasis is very much on the generic abundances of brachiopods that, with the provisos noted above, can be reliably and accurately extracted from the taxonomic descriptions provided in this series of *Treatise* volumes. Indeed, the high degree of standardization of the format of the *Treatise* has allowed automated computer extraction of all the data, including stratigraphic ranges, contained in the taxonomic descriptions (CURRY, CONNOR, & SIMEONI, 2001; CURRY & CONNOR, 2007). This is a result of adopting a standard method of citing stratigraphic ranges, which first lists the overall range in systems and stages, and then cites precise ranges in different geographic areas. Italicizing these data, enclosing stage names in parentheses, and separating them with a colon from the geographic range not only provides a very brief but informative overview for the readers (e.g., *Lower Devonian (Emsian)–Middle Devonian (upper Givetian):* Europe, Central Asia, China, USA (Nevada) (KAESLER, 2002, p. 1444), but also allows the development of computerized techniques to find and extract this information automatically from raw data with such a high degree of internal structure (Curry, Connor, & Simeoni, 2001; Curry & Connor, 2007).

The nature of the raw data available for analysis varied during the course of the study. For some genera, the stratigraphic data were extracted from the full taxonomic description provided in Microsoft Word™ files provided by the *Treatise* editorial office. For other genera, we were provided with text files by Jill Hardesty, assistant editor for the *Treatise,* which included just the taxon name and the cited stratigraphic range. Stratigraphic information was also available for recently described, amended, or corrected, generic data in volume 6 of this *Treatise* (herein, p. 2532–2821), and these data have been included in the analyses presented in this chapter. A complete listing of the stratigraphic range of each taxon is included elsewhere in this *Treatise* (herein, p. 2966–3081). Whatever the source and the extent of initial processing, all the stratigraphic data were formatted in an identical fashion by the contributing authors and editors and were transferred by us into Microsoft Excel™ spreadsheets for analysis and preparation of graphs. These software packages have the advantage of being very commonly used and allowing all necessary graphical interpretations of the compiled stratigraphic data for the purpose of this chapter.

Table 40 provides a summary of the conventions used to analyze all of the stratigraphic data included in the taxonomic descriptions of brachiopod genera, including the ages assigned to each stage (in this chapter a few diagrams plotted using absolute time ordinates use the inferred midpoint ages listed in Table 40). Such a diagram will be important when using stratigraphic data from this *Treatise*, as it provides a snapshot of the prevailing stratigraphic zonation when some systems had already been subdivided into well-established stages, while others were yet to achieve formalized chronostratigraphic unit boundaries. In addition, it has already become quite difficult to obtain copies of the 1989 IUGS chart, so incorporating information on the precise stratigraphic units used in compiling this chapter is essential for future work. For the most part, the units of analysis are formally identified stages, based on internationally agreed subdivisions of the geologic record. Since the compilation and publication of the previous *Treatise* in 1965 (Moore, 1965), there has been a considerable advance in the standardization of the stratigraphic units, notably in the replacement of regional schemes (e.g., European, North American, Russian, Chinese) by a single, well-defined, chronostratigraphic scale that is applicable globally.

Even this approach is not without its complications. There are systems in which the formal stages presented in the 1989 IUGS chart were not universally agreed or recognizable, as is inevitable in a constantly evolving field of research. This was most apparent for the Ordovician and Silurian Systems during the current analysis. For example, many descriptions of Ordovician brachiopods utilized series names (such as Tremadoc, Arenig, Llandeilo-Llanvirn, Caradoc, Ashgill), but for this analysis such citations had to be plotted onto the appropriate stage or stages. Taxa therefore cited as being present in the Caradoc Series were, in practice, entered in the database as being present in the 7 stages within the Caradoc in the 1989 chart (Costonian, Harnagian, Soudleyan, Longvillian, Marshbrookian, Actonian, Onnian). Such a process probably explains why some major features of brachiopod diversity over time occur over several time intervals and are not constrained to a single stage.

Furthermore, in 1989 there were some series without defined stages, for example the Tremadoc and Llarnvirn-Llandeilo, and in these cases the series names were used. Similarly, the widely utilized name Arenig has been used despite the fact that Fennian–Moridunian and Yapeenian–Bendigonian were local names assigned to this interval (neither of which appeared in the brachiopod taxonomic descriptions). Most of the series and stage names for the Ordovician used here have disappeared from *A Geologic Time Scale 2004,* and indeed there are several unnamed stratigraphic units awaiting formal naming by the International Commission on Stratigraphy (Gradstein, Ogg, & Smith, 2004). The nomenclature used here is still common in the literature, is widely used and understood, and hence should be readily transferred onto any future classification. Using such procedures and adopting the conventions shown in Table 40 to plot unconventional stratigraphic data onto the standardized 1989 stratigraphic column resulted in a matrix of the number of genera present in each stage, and this was used to prepare the diagrams presented in this chapter.

ESTIMATES OF BIODIVERSITY?

Although the graphs presented here have been generated from stratigraphic range data, there is a strong inclination to analyze the resulting graphs as indicators of the biologic diversity of brachiopods through time. In reality, there are considerable difficulties in using stratigraphic ranges as measures of taxonomic diversity. The brachiopod community has long discussed the techniques used to analyze stratigraphic data (Cooper & Williams, 1952; Williams, 1965b; Ager, 1988). Extensive literature on the topic has addressed the problem and suggests a range of different metrics to generate more accurate estimates of biodiversity from the raw stratigraphic data. These include mathematic procedures such as normalizing the data to account for the fact that results are biased because taxa are rarely present throughout the entire stratigraphic unit in which they appear and disappear (Sepkoski, 1975). A recent test of some of these techniques (Cooper, 2004) using a model dataset indicated that total diversity (counts of the total number of taxa present in each stratigraphic unit) tended to consistently overestimate actual diversity (i.e., in the model test set of stratigraphic ranges). This phenomenon declined in significance, however, when higher taxonomic units (e.g., genera) and shorter time periods were used (decreasing the number of taxa that are present in only part of a time period; Cooper, 2004).

The procedures adopted in this chapter will no doubt overestimate the actual biodiversity but probably not to a significant extent. In any event, the major interest in the data presented here lies more in trends and patterns than in absolute diversities or inferences about the rates of evolutionary change. Using the total number of genera recorded in each stage will, on the available evidence, most likely enhance trends and patterns without distorting them significantly. This approach has the added value of ensuring that future investigators are completely clear about the methodology used, without the complication of data processing procedures that may well evolve with time.

Simple counts of numbers will not take into account the relative abundance of taxa, so although the first and last appearance of a genus that dominates a fauna is of far greater biological significance than that of a genus with very few fossilized individuals, both will carry a similar weighting in the analyses. Furthermore, it is entirely possible to overlook turnover events in geologic history, because the replacement of established taxa by an equal or very similar number of newly evolved stocks will not show up as a biotic turnover event but will instead look like stasis. Other factors having a major influence on the interpretation of stratigraphic distribution curves, in terms of real biological or environmental events, are the degree to which rocks of a particular geologic system have been exposed at the Earth's surface over the last 200 years or so and the extent to which brachiopods are preserved in the rocks that have been available for study over that period. The early onset of silicification, for example, has clearly had a significant effect on stratigraphic abundances of brachiopods (e.g., the enormously diverse North American Glass Mountain faunas in the Permian; Cooper & Grant, 1969, 1974, 1975, 1976a, 1976b). Similarly it has been suggested that major events such as extinctions in the fossil record are primarily the result of intervals in which widespread marine transgressions have preserved marine strata that are often destroyed during low-stand periods. In effect therefore, these events may be artefacts of the fossil record due to unequal exposure and preservation, various other biases resulting from geologic processes, and as a result of preferential collection or monographic treatment (Cooper & Williams, 1952; Sheehan, 1977; Grant, 1980; Smith, 2001; Smith, Gale, & Monks, 2001; Benton, 2004).

Such complications, however, are primarily relevant for interpretations of biodiversity through geologic time. In this chapter, great care has been taken to distinguish between cited stratigraphic distribution, which at the time of the *Treatise* census is as accurate and standardized as any such data can be, as compared with the much more speculative interpretations and discussions. The former will stand the test of time, while the latter are likely to change to a greater or lesser extent in future years, with improvements in our understanding of the effects of taxonomic procedures and geologic processes on the completeness of the fossil record. Interpretations that correlate patterns of abundance to biological or environmental causes should be considered as speculative and possibly, at best, coarse-scale interpretations applicable only to major events. An alternative approach, taking the data presented here and studying the life-style and morphological characteristics of the taxa concerned and the exposure and preservation of the host stages and systems, may prove a much more productive line of enquiry into the validity and causes in brachiopod diversity over time. Throughout this chapter, the use of the term diversity should be interpreted as referring to the stratigraphic diversity of taxa rather than genuine biological diversity, unless explicitly stated otherwise.

Environmental Proxies

Since the publication of the first brachiopod *Treatise* in 1965 (Moore, 1965) the use of geochemical and isotopic measurements from rocks and fossils has increased dramatically. New techniques are constantly adding to the spectrum of proxies that can be measured to reveal information about environmental conditions far back in geologic time, for which direct evidence is lacking or extremely rare. Refinements and greatly extended usage of isotopic data (such as stable oxygen and carbon isotopic ratios that are expressed as $\delta^{18}O$ and $\delta^{13}C$) has provided important new data on major changes in environmental conditions over geologic time and of the consequences of such changes on life in the past. Such paleoenvironmental reconstructions are all the more valuable when the correlation between the isotopic compositions of the biominerals in a shell has been comprehensively investigated to confirm that it accurately reflects the isotopic composition of the surrounding seawater. The shells of a number of organisms investigated in this way have proved not to be in equilibrium with the surrounding seawater, and such complications, known as vital effects, will distort any paleoenvironmental reconstruction. The low-magnesium shells of calcareous brachiopods have been subjected to extensive isotopic investigation in Recent seas, however, and large parts of their skeletal ultrastructure have proved to be in equilibrium with the surrounding seawater, hence justifying the widespread use of brachiopod shell isotopic compositions as paleoenvironmental indicators in the geologic record (e.g., Veizer & others, 1999; Parkinson & others, 2005; Parkinson & Cusack, herein, p. 2522–2531). Undoubtedly, however, the validity of such determinations becomes progressively more uncertain in specimens of increasing age. There are many different types of geochemical and isotopic proxies, and some of them, such as determinations of strontium isotope ratios, have not only provided a valuable new tool for global stratigraphic correlation but have also generated new insights on the major trends in planetary dynamics (VEIZER, 1989).

This chapter briefly discusses the extent to which the apparent changes in brachiopod diversity over time can be correlated to Earth history events that are either well documented or inferred from proxy data. Comprehensive coverage of what is now an enormous area of research cannot be included here, but clearly it is of great interest to at least note the degree to which investigations of ancient environmental conditions provide possible explanations for the observed distribution of brachiopods through time. For example, intervals where brachiopod diversity changed significantly in apparent synchroneity with major climatic events, as they are presently understood, could plausibly be interpreted as being more reliable records of genuine biological responses to environmental stimuli than those that are not obviously correlated with such events. Conversely, climatic and paleo-oceanographic interpretations will undoubtedly be refined and changed in future years, and it will be intriguing to investigate to what extent the data presented here is consistent with or contradictory to any future developments.

OVERALL DISTRIBUTION

Figure 1912 shows the overall distribution of all brachiopod genera as compiled from the taxonomic descriptions included in the revised *Treatise*, volumes 2 to 6. For comparison, Figure 1913 shows a reconstruction of the hand-drawn stratigraphic distribution chart published in the 1965 brachiopod *Treatise* (WILLIAMS, 1965b, fig. 149). For the most part, the available data in the 1965 chart were collated in terms of lower, middle, and upper subdivisions of each system, and for this study the number of genera in each subdivision was extracted from the 1965 diagram (WILLIAMS, 1965b, fig. 149) and the resulting data used to prepare Figure 1913.

The most recent compilation of brachiopod genera presented in this revised *Treatise* includes records for a total of 4218 genera that are valid for analysis using the stratigraphic and taxonomic criteria discussed above (i.e., ignoring uncertain taxa or distributions). This compares with around 1650 genera recorded in the 1965 *Treatise*, representing an increase of over 2500 genera, or 155%, over the last 41 years. The number of genera in the revised *Treatise* represents an even more dramatic rise, as this analysis excludes all genera with questionable validity and stratigraphic information, and in reality the number of brachiopod genera has probably tripled between the 1965 *Treatise* and this revision. Using the 113-point scale, the 4218 genera analyzed herein generated a total of 17,107 records (i.e., 1 record corresponds to 1 genus present in 1 stage). The 1965 *Treatise* generated about 3000 records, although the use of only 28 census points makes it impossible to directly compare the

FIG. 1912. Cumulative abundance of all brachiopod genera described in the revised brachiopod *Treatise*. The horizontal axis is divided into 113 stages are listed in Table 40 (starting from Tommotian on left through to Holocene on right), and systems are divided by vertical lines (Pleistocene and Holocene stages are unlabelled on the extreme right-hand side of diagram). The term Quaternary is no longer applicable as a convenient grouping, as INQUA has proposed that the Quaternary be formally defined to include the Pleistocene, the Holocene, and the upper part of the Neogene (GRADSTEIN, OGG, & SMITH, 2004). The 113 stages (census points) are equally spaced irrespective of absolute ages assigned to each stage (i.e., they are chronostratigraphic ordinates, and no attempt has been made to incorporate absolute time estimates). Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. Note that the method employed here of displaying the data graphically as an area curve will cause apparent leakage of taxa into later stages as an inevitable result of the curve returning to zero in the stage immediately after the one in which that group of brachiopods was last recorded. The diagram represents an update of that produced for the introduction to volume 5 (KAESLER, 2006, fig. 1101) and includes several thousand more stratigraphic records following the stratigraphic information available on recently described genera and the amended stratigraphic information on previously described genera (as published herein, p. 2532–2821) (new).

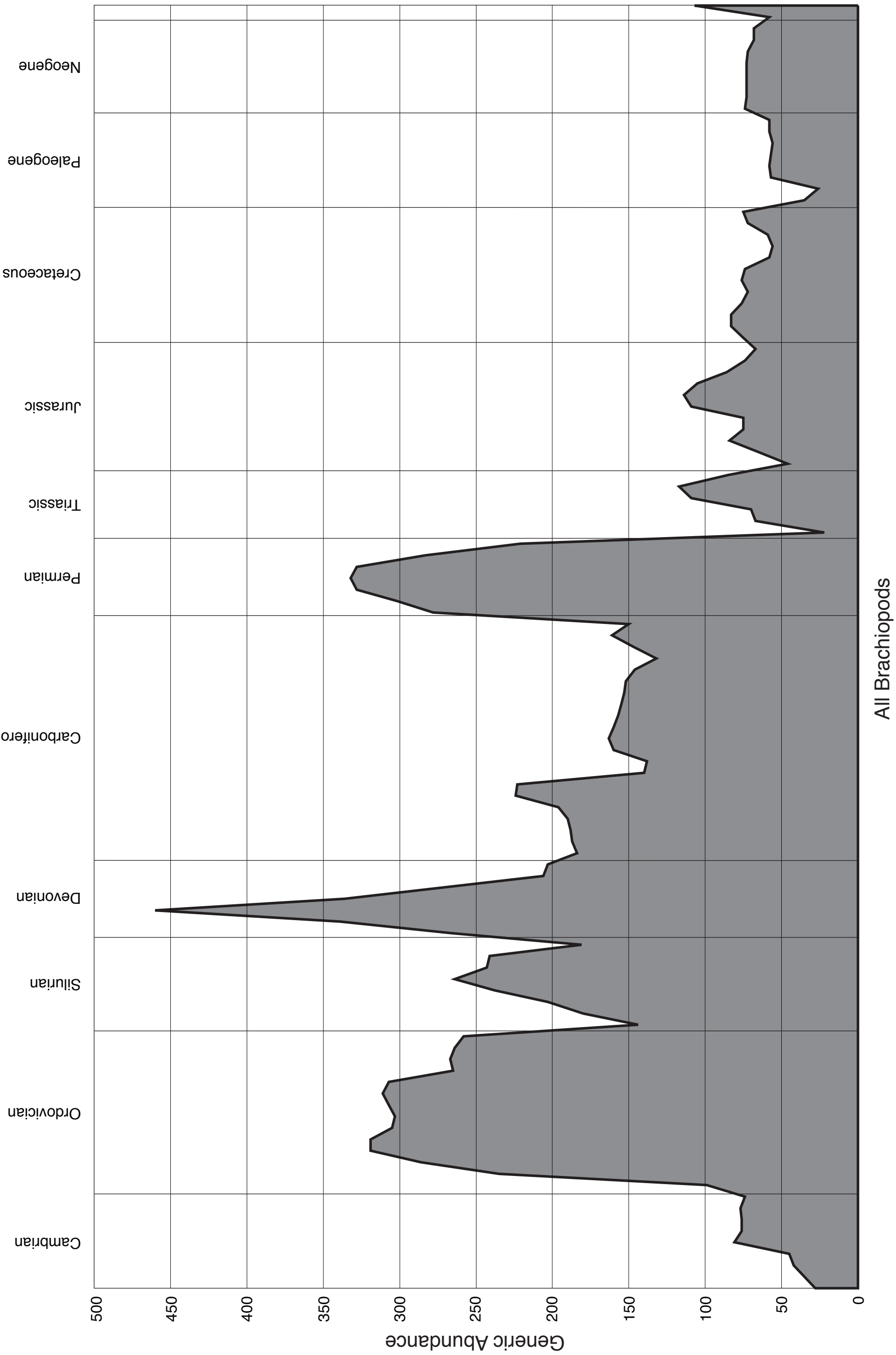

FIG. 1912. *For explanation, see facing page.*

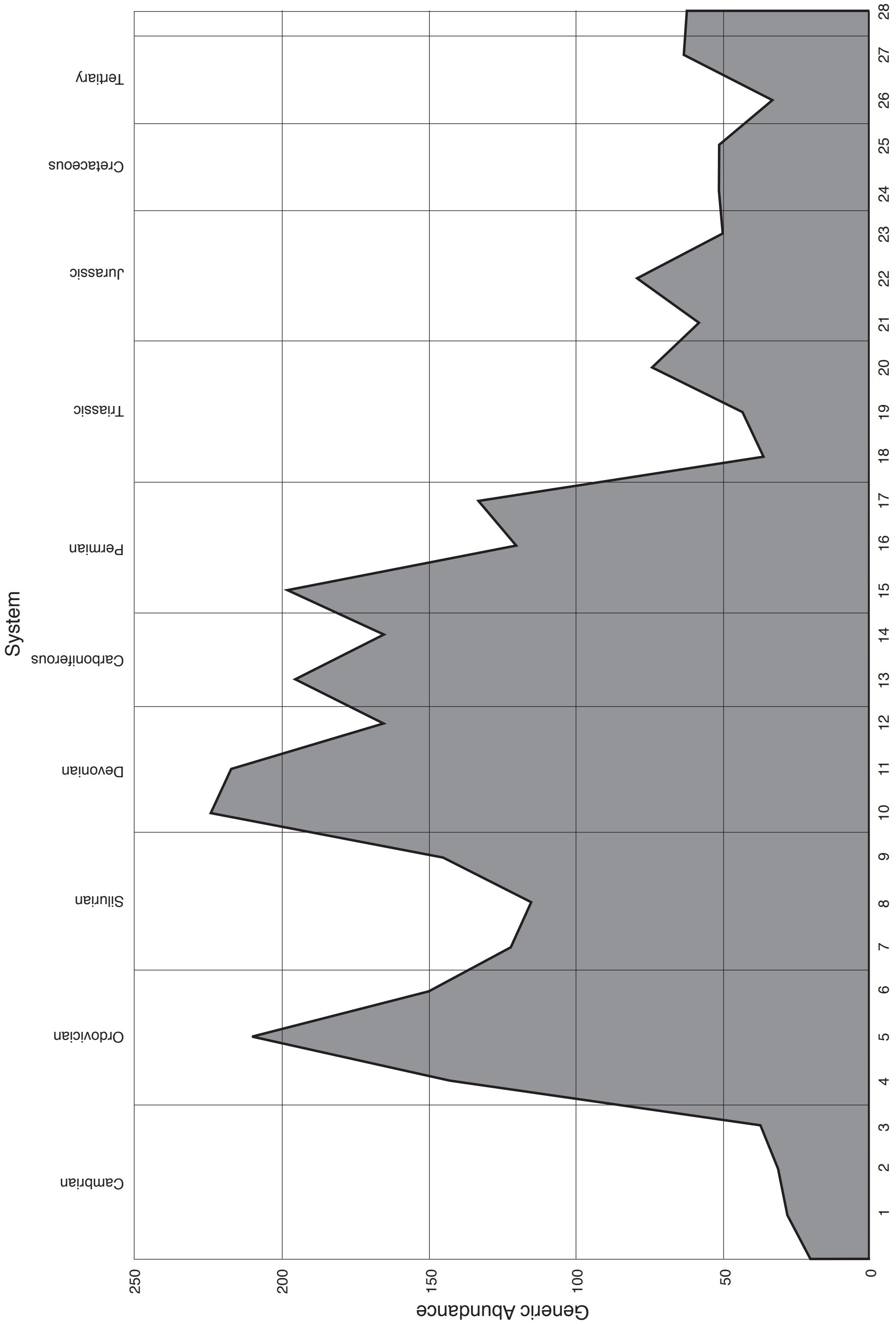

FIG. 1913. *For explanation, see facing page.*

two data sets (for example, an extreme case would be when a single record in the 1965 *Treatise* [Upper Ordovician] is now represented by 11 records [each corresponding to a single stage] in the current analysis).

The overall distribution pattern is similar in both graphs: a slow increase during the Cambrian followed by a rapid increase in generic numbers during the Lower Ordovician, maintaining a comparatively high level of diversity throughout the Silurian, Devonian, Carboniferous, and Permian, with a number of intervals when diversity decreased sharply and then recovered. The greatest decrease in numbers occurred at the end of the Permian, after which the generic diversities of brachiopods never approached the levels of diversity seen throughout the Paleozoic. The Mesozoic and Cenozoic stages, while still showing significant fluctuations, are characterized by diversity of the order of 50–100 genera, as compared with peaks of diversity ranging from 250 to over 450 genera in the Paleozoic. The major changes, such as in the number of ordinates in each system (from 2 to 21 census points in the Carboniferous in the most extreme case), have not seriously distorted the overall pattern of diversity (i.e., higher generic numbers are present in the Lower Carboniferous compared to Upper Carboniferous in the original and the revision of the *Treatise*). Whatever they indicate, it is encouraging that the overall pattern of brachiopod diversity throughout the Phanerozoic has proved to be robust, despite the big increase in the number of genera, the modifications that have occurred in stratigraphic nomenclature, and many other changes that have occurred over the last 40 years.

A comparison of the two graphs clearly reveals the impact of much greater stratigraphic resolution adopted for the current *Treatise*. The peak of brachiopod diversity falls within the Lower Devonian in both graphs, but the greater resolution in Figure 1912 reveals that, while brachiopod diversity was increasing throughout the earliest Devonian (i.e., the Lochkovian and Pragian Stages), the peak of diversity actually occurred within the Emsian Stage (Fig. 1912). The new data present in this chapter reveal that this peak in the Emsian dominates the distribution to a much greater extent than in the 1965 *Treatise,* and the number of genera have more than doubled, from a maximum of 224 for the Lower Devonian in 1965 to 460 for the Emsian Stage in the revised *Treatise*. The rapid Emsian increase in generic numbers was followed by a progressive and equally rapid decline of taxa during the Middle and Late Devonian (Eifelian, Givetian, and Frasnian Stages). The number of brachiopod genera becomes much more stable in the latest Devonian stage (the Famennian) and then increases at a much more modest rate during the Lower Carboniferous. A plot of this data using absolute age ordinates (Fig. 1914) yields a very similar overall curve, with the most obvious difference being the much more gradual slope for the Lower Ordovician increase in the number of brachiopod genera (because of the long duration of the Lower Ordovician stages, as discussed above and in the following sections).

Direct comparisons between the 1965 and 2007 totals are not entirely meaningful, as the former represents the total number of genera in the Lower Devonian (i.e., a

Fig. 1913. Cumulative abundances of brachiopod genera recorded in the first brachiopod *Treatise*, reconstructed by measuring and extrapolation from figure 149 in Williams (1965b); raw data used to construct the original 1965 graph is not available. The census points along horizontal axis are, in sequence from left-hand side of diagram: (1) Lower Cambrian, (2) Middle Cambrian, (3) Upper Cambrian, (4) Lower Ordovician, (5) Middle Ordovician, (6) Upper Ordovician, (7) Lower Silurian, (8) Middle Silurian, (9) Upper Silurian, (10) Lower Devonian, (11) Middle Devonian, (12) Upper Devonian, (13) Lower Carboniferous, (14) Upper Carboniferous, (15) Lower Permian, (16) Middle Permian, (17) Upper Permian, (18) Lower Triassic, (19) Middle Triassic, (20) Upper Triassic, (21) Lower Jurassic, (22) Middle Jurassic, (23) Upper Jurassic, (24) Lower Cretaceous, (25) Upper Cretaceous, (26) Lower Tertiary, (27) Upper Tertiary, (28) Quaternary (unlabelled section on the extreme right-hand side of diagram) (new).

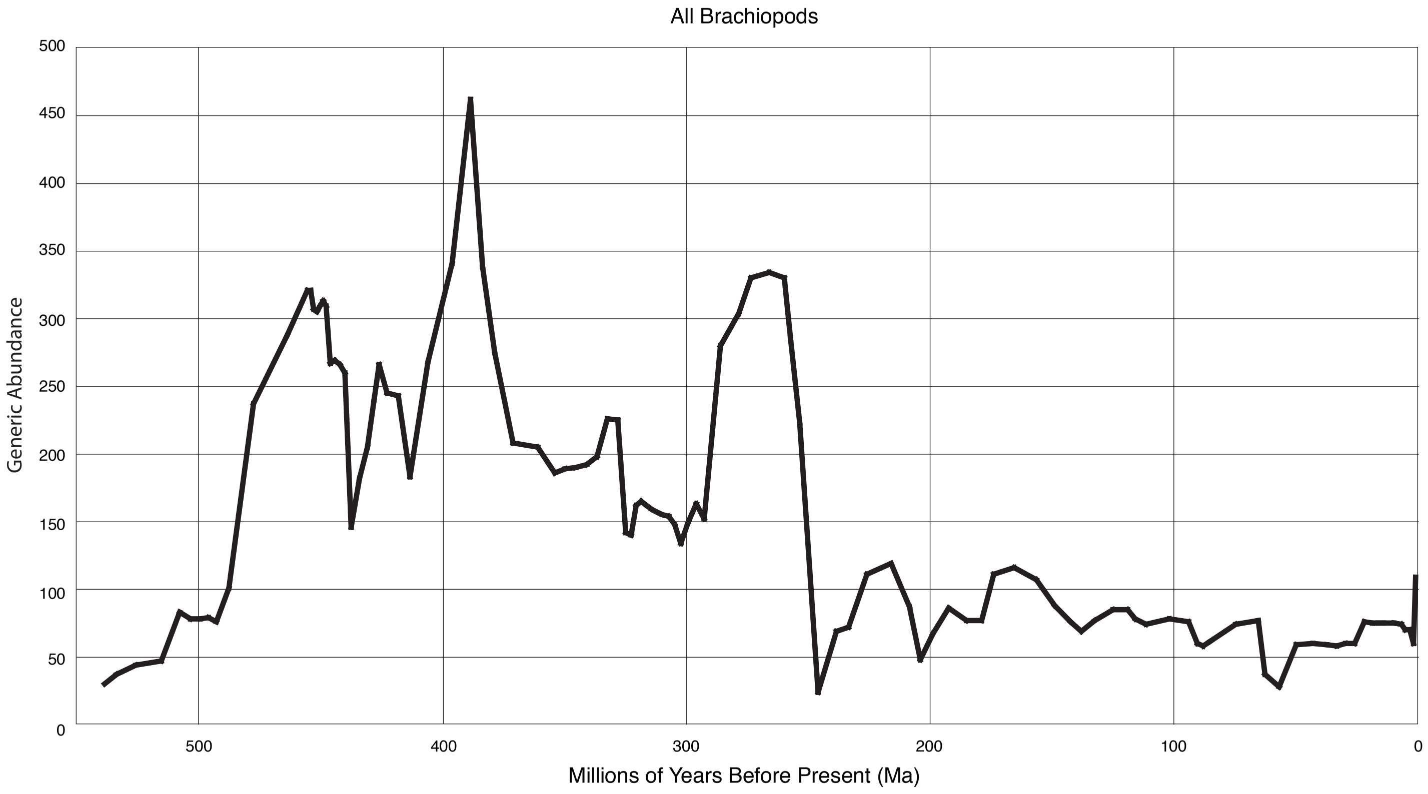

FIG. 1914. Cumulative plot of generic abundances of brachiopods in 113 stages, plotted according to absolute age determinations for the midpoint of each stage. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. This graph plots same data as used in Figure 1912 but uses absolute age ordinates on horizontal axis rather than equally spaced stages (new).

total of 3 stages), while the latter represents the total number of genera recorded in a single stage. In reality, therefore, the increase in brachiopod genera in the Lower Devonian over the last 40 years is even more dramatic, as the total number of distinct genera recorded from the three stages of the Lower Devonian in the revised *Treatise* would be even greater than 460.

Figure 1912 demonstrates that the Roadian Stage of the Permian System has the second greatest diversity of brachiopod genera and that the Costonian Stage of the Ordovician System has the third greatest diversity. Again, this is similar to the pattern seen in the 1965 *Treatise*, but the maximum number of genera has increased by about a third in both cases (again with the proviso that the 1965 figures represent the diversity of the Lower Permian and Lower Ordovician respectively rather than the Roadian and Costonian Stages). In 1965 the Ordovician had the second greatest diversity of any system, but in 2007 the Permian System has slightly more brachiopod genera than the Ordovician System (332 genera as compared with 319).

One striking feature of the stratigraphic data presented here is the extent to which many of the systems begin and end with significant decreases in the numbers of brachiopod genera (Fig. 1912). Such a phenomenon is at least partly a legacy of the historical use of major biological turnover events in the geologic record to define major stratotype boundaries. Note that the method employed here of displaying the data graphically as an area curve will cause apparent leakage of taxa into later stages as an inevitable result of the curve returning to zero in the stage immediately after the one in which that group of brachiopods was last recorded. In Figure 1912 the lines separating systems have been drawn midway between the last stage of one system and the first of the succeeding system. Other differences between the 1965 and 2007 *Treatise* data, such as the dramatic increase in generic diversity during the Permian System and the equally dramatic decline into the Triassic, will be discussed in the appropriate section below.

EXTINCTIONS AND RADIATIONS

Throughout the stratigraphic column, as it was defined in 1989 (Table 40), there are 18 stages (out of a total of 113) in which more than 10% of the genera in the previous stage disappeared from the geologic record. A further 29 stages saw the number of genera increase by over 10% compared to the preceding stage. Brachiopod stratigraphic history is therefore characterized by extensive change. In a total of 47 stages out of a total of 113 (i.e., 42%), brachiopod diversity increased or decreased by 10% or more as compared with the previous stage. Throughout their geologic history, the number of brachiopod genera changed by an average of 6.3% from one stage to another. What is unknown, of course, is the extent to which artefacts, both geologic and human, have contributed to this pattern of apparent extinctions and radiations; and several authors have debated the issue (Ager, 1988; Smith, 2001; Smith, Gale, & Monks, 2001).

What is clear from the analyses presented here is that, in absolute terms, there are 14 stages where 20 genera or more disappear, and 22 stages in which 20 genera or more are added to global diversity of the phylum. Again, the pattern is for the number of brachiopod genera to be noticeably changeable throughout the Phanerozoic, with 32% of stages recording either an increase or a decrease of 20 or more genera.

The most significant extinction event in brachiopod history was at the Permian-Triassic boundary. Over 90% of the genera present in the Changhsingian disappeared at the end of stage, and this event was also the largest in brachiopod history in absolute terms (199 genera disappear). The end-Emsian (Devonian) was the second largest extinction event in brachiopod history in absolute terms (124 genera disappeared), but it was much less significant (27%) in percentage terms. The end-Hirnantian (Ordovician) decline (114 genera) was the third greatest in brachiopod history, and also the third most significant in percentage terms (44%). The end-Cretaceous was the second largest apparent extinction in brachiopod history in terms of percentages (53%) but involved the disappearance of only 40 genera, so was low in terms of absolute numbers of genera disappearing. In addition to the end-Permian, end-Emsian, and end-Hirnantian events, there are a further five stages that witnessed more absolute generic reductions than the end-Cretaceous event: end-Capitanian: 62 genera; end-Wordian: 45 genera; end-Brigantian: 83 genera; end-Givetian: 67 genera; end-Onnian: 42 genera. Major radiation and extinction events are discussed in more detail in the sections that follow; there is also extensive literature on the subject (e.g., AGER, 1987; BOUCOT, 1996; MACLEOD & KELLER, 1996; SHEN & SHI, 1996; BASSETT, POPOV, & HOLMER, 1999; DULAI, 2001; CHEN, SHI, & KAIHO, 2002; MACLEOD, 2003; MILLER, 2004; ALVAREZ, 2006; HARPER, 2006).

CAMBRIAN SYSTEM

The Cambrian System (542 ± 1.0 Ma to 488.3 ± 1.7 Ma; GRADSTEIN, OGG, & SMITH, 2004) is subdivided into nine stages (Table 40), and the numbers of brachiopod genera increase progressively but slowly from the Lower Cambrian Tommotian Stage (a total of 28 genera recorded) through to 45 genera in the uppermost Lower Cambrian Toyonian Stage (Fig. 1915). The Amgaian Stage is characterized by a significant increase in brachiopod genera, with 81 genera recorded. With minor fluctuations, the number of brachiopod genera found in the subsequent stages of the upper Middle and Upper Cambrian stages remains relatively constant at around 75 genera.

The brachiopod faunas in the Cambrian are taxonomically diverse. Overall the system contains representatives assigned to no less than 12 different orders out of a total of 26 orders described for the entire phylum. For the entire Cambrian System, brachiopods assigned to the Lingulida and Acrotretida are dominant, together representing over half the total diversity (Fig. 1916).

Four out of a total of 26 brachiopod orders are restricted to the Cambrian System (the Kutorginida, Naukatida, Obolellida, and Chileida), and all disappeared by the end of the Middle Cambrian. The Chileida and the Naukatida last appear in the lowermost Amgaian Stage of the Middle Cambrian, while the Kutorginida and the Obolellida make their last appearance in the uppermost Mayaian Stage of the Middle Cambrian. None of these orders are represented by large numbers of taxa, with a maximum, in any one stage, of 8 Obolellida genera, 8 Kutorginida genera, 3 Chileida genera, and 2 Naukatida genera (Fig. 1916). These orders were a significant, but short-lived, component of the Cambrian explosion and the Paleozoic fauna (SEPKOSKI, 1975). Although relatively trivial in number, these genera are important for what they tell us about the tremendous burst of evolutionary innovation and diversification in the Lower Cambrian.

While some of the orders that appeared in the Lower Cambrian had a short geologic history, others were represented by increased numbers of genera in the Upper Cambrian stages (Fig. 1916). The Lingulida and the Acrotretida in particular radiated markedly during the Upper Cambrian, and although the diversity of both declined sharply at the end of the Cambrian, both orders subsequently recovered during the Lower Ordovician. Together with the two other orders that constitute the Linguliformea (the Paterinida and the Siphonotretida), the subphylum achieved its maximum diversity during the Lower Ordovician.

Examining the taxonomic diversity of brachiopods present in different stages of the Cambrian demonstrates considerable variability. The Lower Cambrian Tommotian

Stage is dominated by Lingulida (21%) and Obolellida taxa (21%), while the Paterinida (14%), the Kutorginida (14%), and the Protorthida (14%) also represent significant contributions to the overall brachiopod generic abundances that include representatives of a total of 8 orders (Fig. 1916). The Naukatida first appeared in the Botomian Stage, and so by the uppermost Toyonian stage of the Lower Cambrian a total of 9 orders were represented by the 45 genera recorded, and the Lingulida had become the dominant order (33%), followed by the Kutorginida (16%) and the Obolellida (11%).

The comparatively large increase in the number of brachiopod genera recorded in the Amgaian Stage (lowermost Middle Cambrian) reflected not only the appearance of two new orders (the Pentamerida and the Billingsellida, bringing the total number of orders to 11) and the continuing dominance of the Lingulida, but most significantly, great increases in the numbers of Acrotretida (from 11% in the Toyonian to 27% in the Amgaian) and the Orthida (2% in the Toyonian to 16% in the Amgaian). The remainder of the Cambrian was characterized by a very similar number of genera but a decrease in overall diversity, down to 7 orders by the end of the Cambrian. Indeed, the Middle Cambrian witnessed the last occurrences of no less than 4 orders. The Chileida and Naukatida made their last appearance in the Amgaian Stage, and the Obolellida and the Kurtorginida in the Mayaian Stage. The only example of taxonomic diversification during the Middle Cambrian was the first appearance of the Siphonotretida in the Mayaian. By the uppermost Cambrian the Lingulida and the Acrotretida had become even more dominant constituents of brachiopod faunas (collectively representing 69% of recorded taxa). The Protorthida are absent from the Upper Cambrian but appear again in the Lower Ordovician.

The absolute age range of the Cambrian System has changed significantly since 1989, when the cited duration was from 570 Ma (or 540 Ma, as a result of complications with the correlation of the base of the Tommotian and the Proterozoic–Lower Cambrian boundary) to 510 Ma (a total duration ranging from 60 to 30 million years). The composite time scale adopted here (in which all the stratigraphic units below the Atdabanian were labelled as Tommotian for simplicity; Table 40) has a time span of 540–490 Ma, a total range of 50 million years, which is very similar to that given in the latest compilation of *A Geologic Time Scale 2004* (452 ± 1.0 Ma to 488.3 ± 1.7 Ma = 53.7 million years; GRADSTEIN, OGG, & SMITH, 2004). The Cambrian stages have undergone extensive modification since 1989, however, and there are now a total of 6, although only one of these stages has been formally named (GRADSTEIN, OGG, & SMITH, 2004).

Whatever the complexities of stratigraphic nomenclature, it is clear that brachiopods were taxonomically very diverse at the base of the Cambrian and hence must have an extensive but so far unrecorded or unrecognized Precambrian presence as organisms without a mineralized skeleton. The available data indicates that the diversity and abundance of brachiopods remained virtually unchanged throughout the Lower Cambrian (approximately 30 million years from the base of the Cambrian, using the absolute dates shown in Table 40).

The major change in the number of genera within the Cambrian occurred in the lower Middle Cambrian Amgaian Stage when generic abundances increased by 80% compared to the preceding uppermost Lower Cambrian Toyonian Stage, while overall taxonomic diversity only increased slightly (to 11 orders as compared with 10 in the Lower Cambrian). A sharp excursion in carbon isotope ratio at the Lower to Middle Cambrian boundary has been thought to correlate with a trilobite mass extinction event (MONTAÑEZ & others, 2000). Brachiopods may therefore have radiated in the aftermath of such an event. The stocks that underwent the greatest increase in

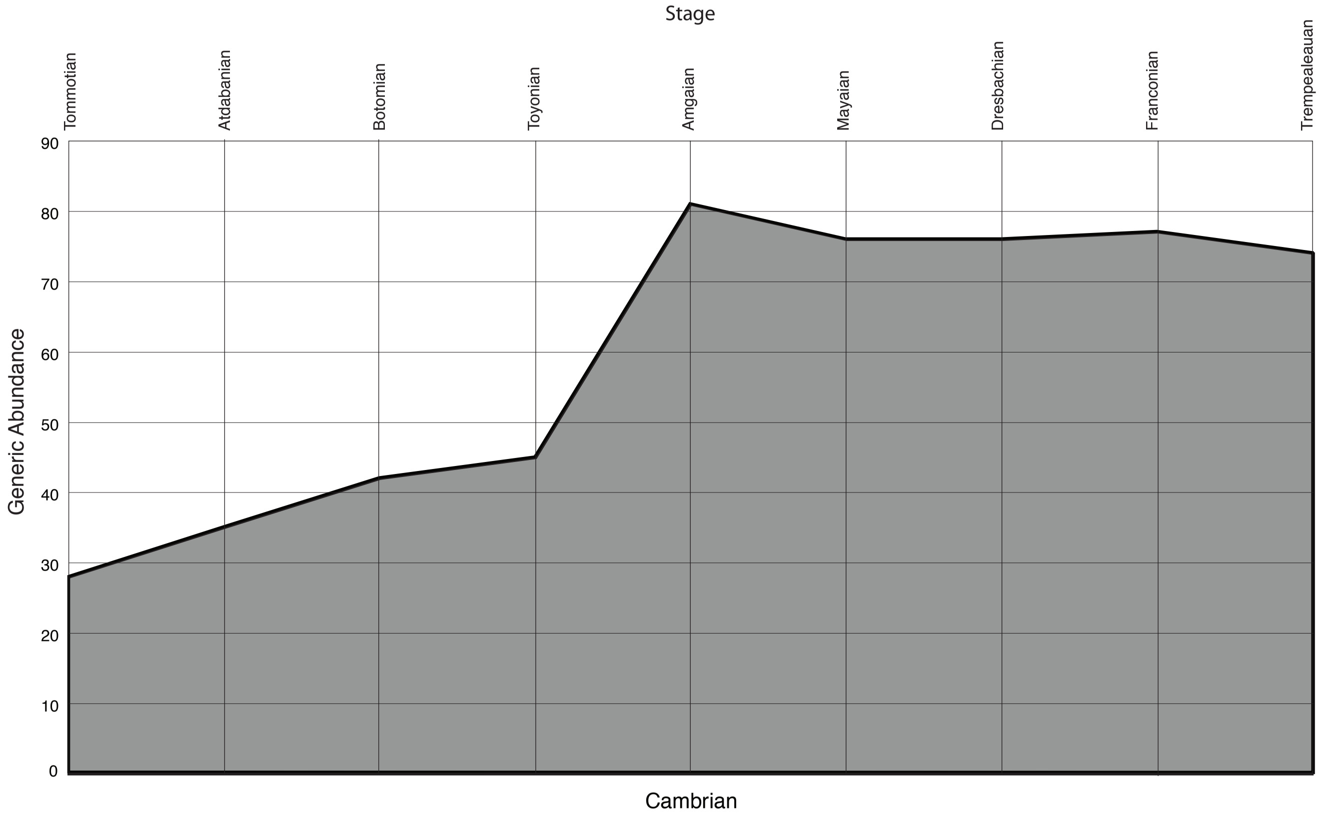

FIG. 1915. Abundance of brachiopods in each of the 9 stages (horizontal axis) assigned to Cambrian System, with lowermost stage (Tommotian) on left-hand side of horizontal axis and uppermost Trempealeauan Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

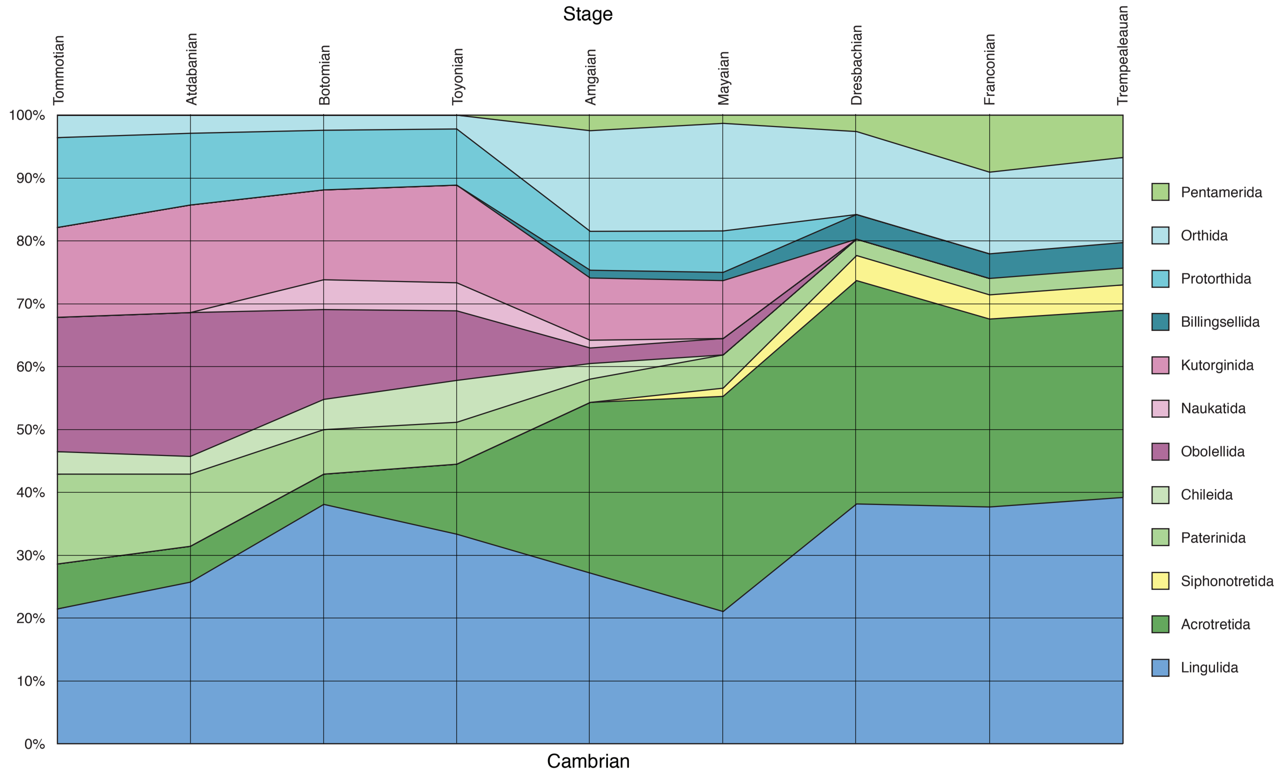

FIG. 1916. Relative proportions of different orders of brachiopods recorded from each of 9 stages of Cambrian System, with lowermost stage (Tommotian) on left-hand side of horizontal axis and uppermost Trempealeauan Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. Key on right indicates different brachiopod orders present (new).

the Middle Cambrian were the Lingulida and the Acrotretida. The increase in the number of the Acrotretida was the most dramatic, from 5 in the Toyonian to 22 in the Amgaian, and the order maintained a level of at least 22 genera throughout the remainder of the Cambrian and reached a maximum diversity of 27 genera in the Dresbachian Stage.

The overall generic abundances of brachiopods are lower in the Cambrian than in virtually any other system throughout the Phanerozoic (with the exception of parts of the Cretaceous, Paleogene, and Neogene; Fig. 1912). In addition, the antiquity, relatively poor preservation, and limited exposure of Cambrian rocks makes it difficult to interpret the Cambrian stocks of brachiopods in anything other than very general terms. Brachiopods are undoubtedly significant and diverse components of the explosion of metazoans that acquired mineralized skeletons in the Lower Cambrian, and the earliest representatives of the subphylum Linguiformea represent some of the oldest known benthic organisms with a mineralized skeleton (Bassett, Popov, & Holmer, 1999). The number of brachiopod genera recorded increased markedly at the beginning of the Middle Cambrian and thereafter remained relatively stable for the remainder of the Cambrian despite the fact that taxonomic diversity declined markedly in the Upper Cambrian. Bassett, Popov, and Holmer (1999) noted that the two most diverse orders of organophosphatic-shelled brachiopods (i.e., the Lingulida and the Acrotretida) were major constituents of the initial Cambrian radiation and, by the end of the Cambrian, had colonized all types of marine depositional environments. Furthermore, during the Cambrian, the Lingulida had spread progressively from predominantly shallow-water habitats to deep-water environments and had become dominant constituents of the faunas in areas of high-energy sand deposition (Bassett, Popov & Holmer, 1999). Indeed, brachiopods were, after trilobites, the second most important constituents of benthic communities in shelf and platform environments during the Cambrian.

Information on the climates and environments in the Cambrian System are sparse; there are, for example, limited isotopic data that could be used as a proxy for environmental change. What is known about the conditions on Earth suggests comparatively warm climates prevailed globally (Montañez & others, 2000), implying that there were no significant glacioeustatic changes in sea level that might have had a discernible effect on brachiopod diversity. There is clear faunal provinciality in the Cambrian and tectonic events such as the opening of the Iapetus Ocean and progressive drift of continents toward the equator. It would seem doubtful that global tectonism had a significant effect on brachiopod diversity at the level of resolution of the stratigraphic data presented here. The comparative success of the Acrotretida and Lingulida may have owed more to their morphological adaptability and environmental tolerance of the Cambrian oceans, where conditions would have been very different from those in present-day oceans. It has been suggested that the success of the subphylum Linguliformea in the Cambrian and early Ordovician might be related to their low energy requirement and their tolerance of significant daily fluctuations in the oxygen content of seawater; such attributes therefore allow them to colonize marginal habitats (Bassett, Popov, & Holmer, 1999). Whatever the reason, it is clear that the Cambrian is a system in which there was considerable evolutionary experimentation with several distinct groups arising and dying out relatively quickly.

ORDOVICIAN SYSTEM

Although the Ordovician (488.3 ± 1.7 Ma to 443.7 ± 1.5 Ma; Gradstein, Ogg, & Smith, 2004) saw one of the most significant radiations in the number of brachiopod genera throughout their entire geologic history (increasing to 19 orders, as compared with a total of 12 recorded in the Cambrian), the system started on a subdued note with the Lower Ordovician Tremadoc Stage registering only a slight increase in the total number of genera compared to the Upper Cambrian (Fig. 1917). A total of 99 genera have been recorded from the Tremadoc Stage, as compared with 74 for the uppermost Cambrian Toyonian Stage. The seven orders present in the Tremadoc are the same ones present in the uppermost Cambrian Trempealeauan Stage, although there are some changes in the relative proportions of genera assigned to these orders between the Trempealeauan and the Tremadoc Stage. The most notable changes are in the diversity of the Lingulida and the Acrotretida, which had been dominant in the Upper Cambrian and which would diversify further in subsequent Ordovician stages, but suffered significant decreases in the numbers of genera in the Tremadoc Stage. Much of the increase in the overall number of genera can be attributed to a significant radiation in taxa assigned to the Orthida from the uppermost Cambrian Toyonian Stage (10 genera as compared with 35 genera in the Tremadoc Stage) and the Pentamerida (5 genera as compared with 14 genera in the Tremadoc Stage).

Although the details are intensively debated, there is no doubt that the Ordovician Period was characterized by major fluctuations in both climate and sea level (NIELSEN, 1992). Tremadoc Stage brachiopod distributions may reflect the effects of such changes, as the evidence suggests that there was a major increase in sea level in the lower Tremadoc (a transgression) and an abrupt and pronounced decrease in sea level (a regression) in the middle to upper Tremadoc (NIELSEN, 1992). Oxygen isotope determinations remain essentially level throughout the stage (VEIZER & others, 1999; GRADSTEIN, OGG, & SMITH, 2004), which implies that there were no major global temperature fluctuations, although the sampling interval may have been too large to pick up short-term events that may have influenced brachiopod diversity. If eustatic changes did have an impact on Tremadoc brachiopod faunas, then it is clear that the Lingulida and Acrotretida were disadvantaged, while the Orthida and Pentamerida flourished.

The succeeding Arenig Stage is thought to have started and ended with comparatively low sea levels, but for the majority of its 13 million years, Earth is thought to have experienced high sea levels. Indeed, overall the Ordovician is characterized by comparatively high sea levels, perhaps the highest in the Phanerozoic (FRAKES, FRANCIS, & SYKES, 1992; HALLAM, 1992). Such conditions may well have contributed to the success of the brachiopods during the Arenig, when the diversity more than doubled (to 235 genera) compared with the Tremadoc, and a total of 10 orders were present, when the Craniida and the Strophomenida appeared for the first time (Fig. 1918). The latter order was particularly successful, with 33 Strophomenida genera recorded during the Arenig, while the diversity of the organophosphatic-shelled brachiopods increased significantly during the late Tremadoc and early Arenig Stages (BASSETT, POPOV, & HOLMER, 1999).

It would be too simplistic to regard increasing brachiopod diversity as a reflection of persistent warm climates and high sea levels, because there is considerable geochemical evidence of major environmental perturbations within the Arenig. For example the ^{87}Strontium/^{86}Strontium ratio increased throughout the Ordovician, but at a higher rate in the Arenig than in any other Phanerozoic stage (QING & others, 1998). The steepness of the change, along with coeval variations of a similar nature in the oxygen and carbon isotope signal, have been interpreted as evidence of global oceanic and terrestrial changes (SHIELDS, CARDEN, & VEIZER, 2003). Attempts to correlate periods of significant environmental perturbation with brachiopod diversity are obviously complicated by the long duration of the Arenig.

The Llandeilo-Llanvirn Stage saw continued diversification, with 286 genera representing a total of 15 orders (Fig. 1918).

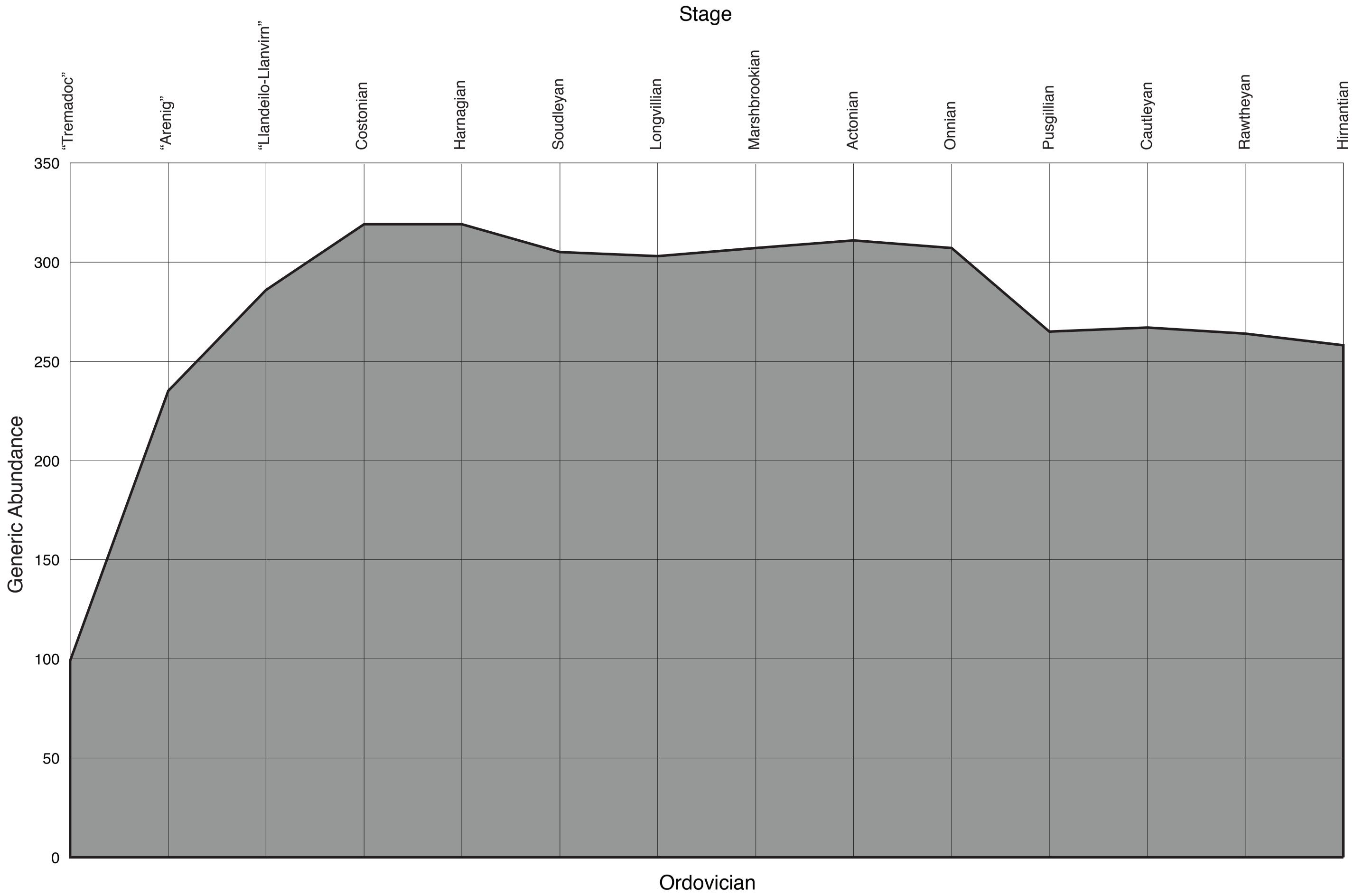

FIG. 1917. Abundance of brachiopods in each of 14 stages (horizontal axis) assigned to Ordovician System, with lowermost stage (Tremadoc) on left-hand side of horizontal axis and uppermost Hirnantian Stage on right-hand side. See Table 40 for stage nomenclature, common abbreviations, meaning of quotation marks, and absolute ages (midpoint, base, and duration) (new).

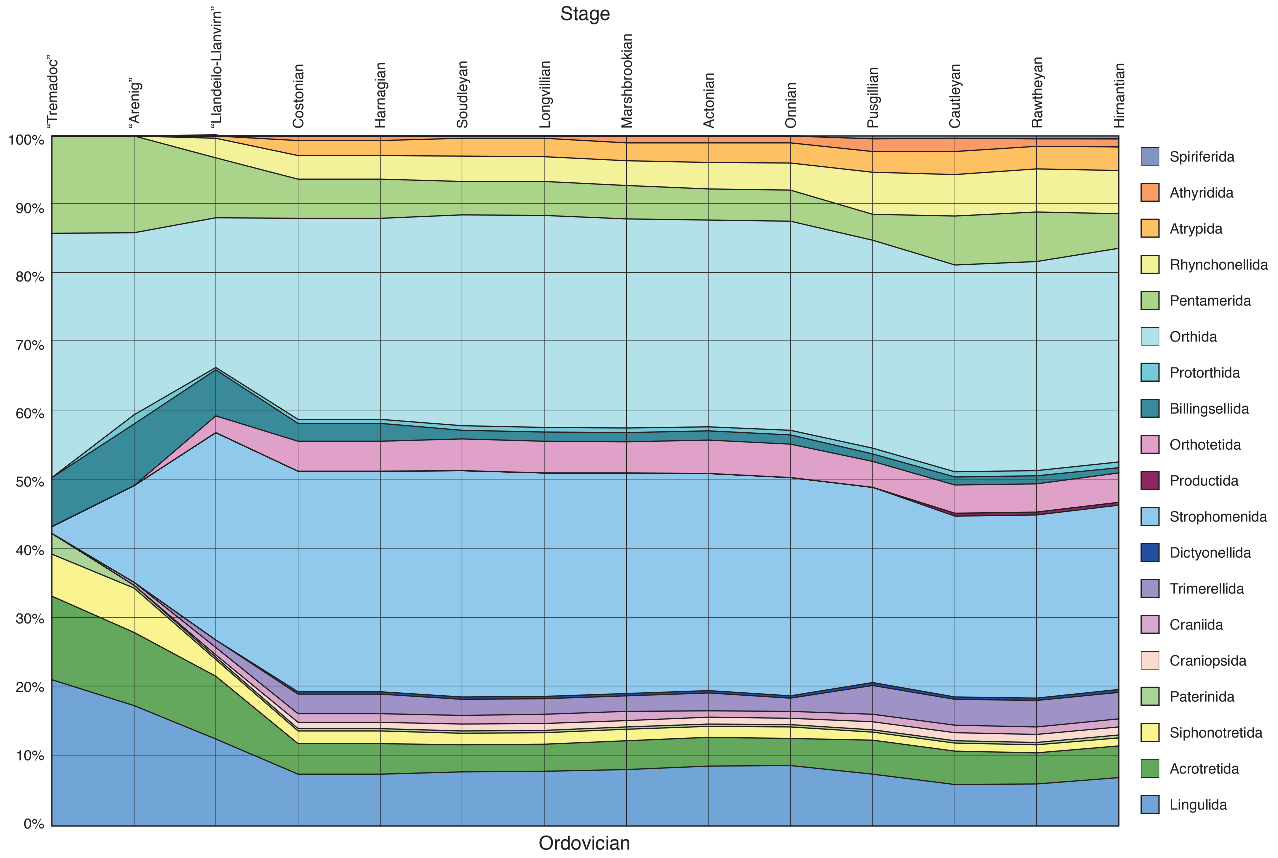

FIG. 1918. Relative proportions of different orders of brachiopods recorded from each of 14 stages of Ordovician System, with lowermost stage (Tremadoc) on left-hand side of horizontal axis and uppermost Hirnantian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present. Some orders are recorded in such low numbers that they are hard to distinguish (for example, Spiriferida and Dictyonellida) but are included in diagram to ensure completeness; see Table 40 for meaning of quotation marks (new).

The Craniopsida, Trimerellida, Orthotetida, Rhynchonellida, and Atrypida all appeared for the first time, although in relatively small numbers. By far the largest change in brachiopod diversity during the Llandeilo-Llanvirn Stage was the continuing dramatic increase in numbers of Strophomenida first apparent in the Arenig; generic numbers increased to 86 (up from 33 in the Arenig). Between 50% and 60% of the organophosphatic brachiopods disappeared during the Llandeilo-Llanvirn, however, and it was particularly noticeable that communities from nearshore and inner-shelf habitats where lingulide brachiopods commonly had an epibenthic life-style were replaced during the Llandeilo-Llanvirn by brachiopod-mollusk assemblages in which the predominant brachiopods were burrowing lingulides (Bassett, Popov, & Holmer, 1999).

The overall trend of increasing generic numbers continued into the succeeding Costonian Stage, reaching a total of 319 genera, the highest of any Ordovician stage. Taxonomic diversity also increased to 17 orders, with the first appearance, in low numbers, of the Athyridida and Dictyonellida. The number of Strophomenida genera continued to increase but more slowly (to 102 genera from 86 in the Llandeilo-Llanvirn), but the most dramatic increase was in Orthida genera (to 93 from 62 in the Llandeilo-Llanvirn). As a result, over 30% of Costonian genera were Orthida. The decline of the Pentamerida, from 33 genera in the Arenig to 25 in the Llandeilo-Llanvirn, continued into the Costonian, and only 18 genera are recorded from this stage. The number of Pentamerida genera fluctuated slightly during the remainder of the system, but there were always fewer than 20 genera in any subsequent Ordovician stage.

The divergence between chronostratigraphic and absolute time ordinates has a particularly strong effect on the perception of the brachiopod's role in the Great Ordovician Biodiversification Event. The use of chronostratigraphic ordinates gives the impression of a very rapid increase in brachiopod generic numbers (e.g., Fig. 1912, 1917). The use of absolute time ordinates, which take into account the much greater duration of Lower and Middle Ordovician stages, demonstrates a much more gently sloping curve (Fig. 1919), testimony to a diversification that remains dramatic but is much more sustained than abrupt. Most of the reorganized Ordovician stages remain unnamed (Gradstein, Ogg, & Smith, 2004), but Ordovician workers have divided the system into a total of 19 time slices that are of much more equable duration (Webby, Cooper, & others, 2004). The use of such time slices as ordinates for stratigraphic charts would certainly refine our understanding of brachiopod history (Harper & others, 2004), but such resolution was not attainable from the data present in the revised *Treatise*. Applying different methods of estimating diversity to alternative data sets produced distributions that differed in small detail but were very similar in overall appearance (Harper & others, 2004).

A variety of environmental factors are thought to have been significant in influencing brachiopod diversity during the Ordovician. Apart from sea level and climate mentioned above, there is evidence that some groups migrated into deeper water (Harper, Rong, & Zhan, 1999), while others radiated into a number of shallow-water carbonate environments (Harper & others, 2004). Some stocks are thought to have first appeared in equatorial regions characterized by a range of separate tectonic plates and numerous volcanic arcs (Popov & others, 1997). The habitats occupied by brachiopods also diversified during the Ordovician (Harper & others, 2004), and the existence of calcitic seas during the period may also have been significant for the diversification of calcareous-shelled brachiopods (Stanley & Hardie, 1999). It does seem as if the reasons for the Ordovician diversification of brachiopods are complex and not yet fully resolved, although clearly worthy of further research. There are extensive publications on this

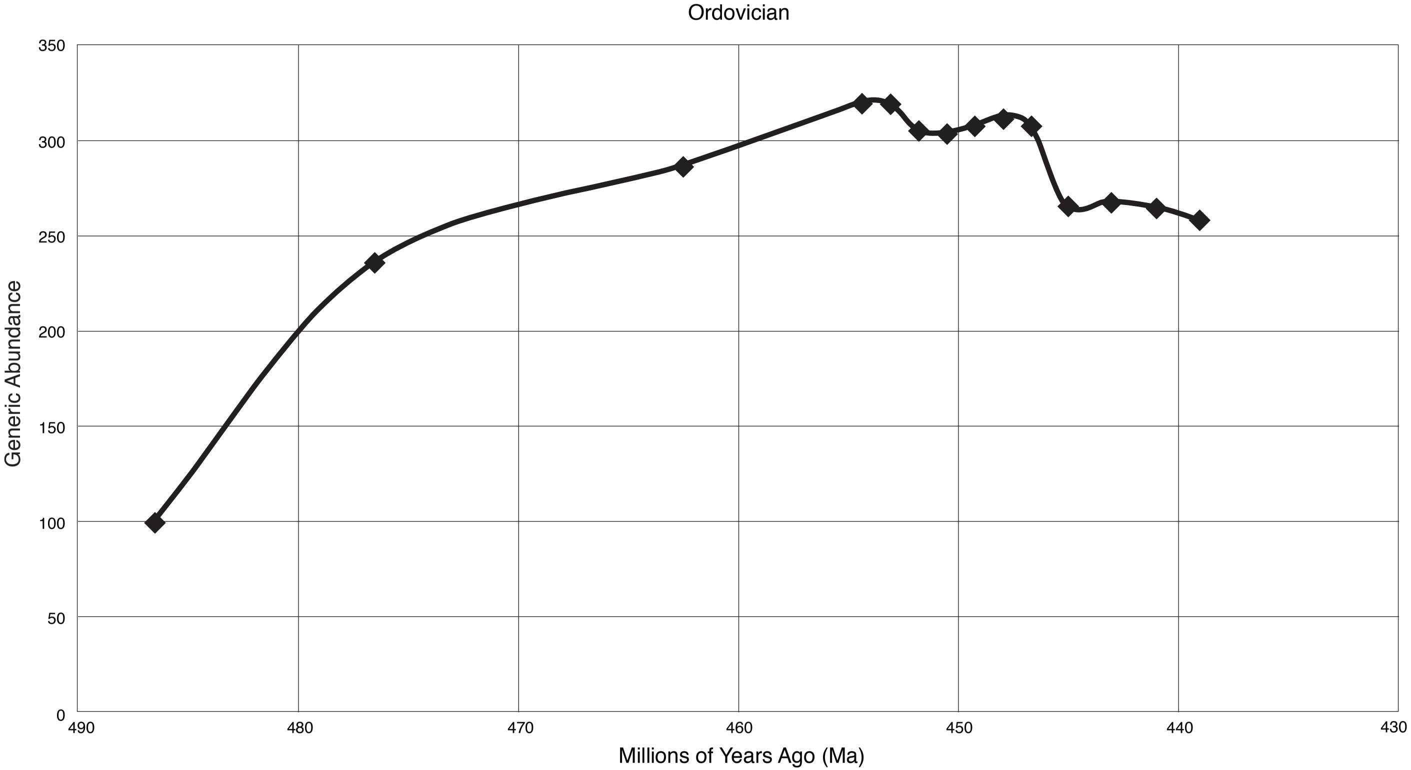

Fig. 1919. Plot of generic abundances of brachiopods in each of 14 stages (horizontal axis) assigned to Ordovician System, with lowermost stage (Tremadoc) on left-hand side of horizontal axis and uppermost Hirnantian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. Graph plots same data as used in Figure 1917, but used absolute age ordinates on horizontal axis rather than equally spaced stages. Diagram demonstrates the much more gradual nature of Ordovician Biodiversification Event than is apparent from plotting data using equally spaced stage ordinates on horizontal axis (i.e., Fig. 1917) (new).

intriguing topic, including the role played by brachiopods and other phyla in the Great Ordovician Biodiversification Event (Webby, Paris, & others, 2004). Among the topics discussed as being of possible significance for the radiation of the brachiopods have been food resources, increases in absolute sizes of individuals, morphological innovation, and exploitation of the phylum of far-reaching changes in the marine communities of the time (Harper & others, 2004). It is also possible that the diversification involved more than one event (Harper, 2006).

After the extensive taxonomic turnover witnessed in the Cambrian and the Lower and Middle Ordovician, the Upper Ordovician was a time of continuity, with little taxonomic change and comparatively constant generic numbers (Fig. 1918). Two new major taxa appeared (the suborder Chonetidina within the Productida in the Cautleyan and the Spiriferida in the Pusgillian), although they are represented by very few genera. By the end Ordovician Hirnantian Stage, a total of 19 orders were represented, although a progressive decline in the number of Strophomenida (down to 69 genera in the Hirnantian from a peak of 102 genera in the Costonian and Harnagian) was the principle reason for a decrease in the overall number of genera to 258 in the Hirnantian Stage (Fig. 1917).

The Hirnantian Stage experienced the culmination of a global cooling event that resulted in high-latitude glaciations (Brenchley, 2004) and a dramatic global extinction event (Sepkoski, 1995) estimated to have seen the demise of over 20% of all families, 60% of all genera, and over 80% of species (Jablonski, 1991; Sepkoski, 1995; Brenchley, 2004). The extinction event occurred in two phases: first, in the lower Hirnantian and second, in the middle and upper Hirnantian (Sheehan, 2001). The sharp decline in numbers of Strophomenida genera in the Hirnantian probably reflects major environmental changes resulting from glaciation. Most of the impact of the event will not show up within the Hirnantian data, as most genera that became extinct during the stage will be recorded as present, even if this was just for a small part of the stage. The Hirnantian ice age is clearly demonstrated in oxygen isotope determinations and confirmed by extensive sedimentary and faunal evidence (Brenchley, 2004).

Other factors that may have had an influence on perceived brachiopod diversity in the Ordovician include the availability of extensive silicified faunas, which almost certainly facilitates the recovery of a much greater proportion of the fauna than is the case with nonsilicified specimens. The role played by silicification is considered in more detail in the section dealing with Carboniferous brachiopod faunas.

SILURIAN SYSTEM

Brachiopod diversities in the initial Rhuddanian Stage of the Silurian (443.7 ± 1.5 Ma to 416.0 ± 2.8 Ma; Gradstein, Ogg, & Smith, 2004) demonstrate the dramatic effect of the Hirnantian glaciation (Fig. 1920). The 144 genera recorded in the Rhuddanian represent a decline of 44% from that recorded in the uppermost Ordovician Hirnantian Stage. Subsequently, the number of genera increased steadily in succeeding stages, almost doubling by the Homerian Stage (to 264 genera), and thereafter declining again to 181 in the Přídolí Stage (Fig. 1920). Three orders present in the uppermost Ordovician Hirnantian Stage (the Siphonotretida, Paterinida, and Billingsellida) did not survive into the lowermost Silurian Rhuddanian Stage, although all three orders were represented by relatively few genera in the Ordovician.

The taxonomic diversity of the brachiopods was high during the Silurian, with representatives of 16 out of a total of 26 brachiopod orders. In the Silurian, the Pentamerida displayed their maximum generic diversity with 52 genera recorded from the Gorstian Stage. There is a relatively small increase in numbers of chonetidine Productida during the Silurian, after having evolved in the Upper Ordovician. No other productides appeared until the lower Devonian. Similarly, the Spiriferinida and Terebratulida did not appear until the Lower Devonian.

A striking feature of the Silurian brachiopod faunas is their taxonomic homogeneity over a period of approximately 28 million years. In all but the last stage there are 16 orders represented (genera assigned to the Trimerellida appear for the last time in the penultimate Ludfordian Stage of the Silurian). The Orthida, Rhynchonellida, Strophomenida, Pentamerida, and Atrypida are dominant in the Rhuddanian Stage and indeed throughout most of the Silurian Period (Fig. 1921). The Spiriferida undergo the most dramatic radiation during the Silurian, increasing from 2 genera in the basal Rhuddanian Stage (1% of the total number of brachiopods in that stage) to 28 genera in the uppermost Přídolí Stage (15% of the total number of genera; Fig. 1921). Indeed, by the Přídolí Stage, the Spiriferida had become the most abundant order (Fig. 1921).

While the number of Spiriferida increased progressively throughout the Silurian, it was the Pentamerida that displayed the greatest variability in numbers, ranging from 16 genera in the Rhuddanian (11% of the total number of brachiopod genera recorded from that stage) to around 50 genera in the Homerian, Gorstian, and Ludfordian (ranging from 19% to 21% of the total) and then declining to 19 genera (11%) in the uppermost Silurian Přídolí Stage.

Thus, the peak of absolute diversity in the Homerian largely reflects the radiation of the Pentamerida and the continued success of the Orthida (to 42 genera [16%] from 36 in the Rhuddanian [25% of the lower absolute number of brachiopods recorded from that stage]). As occurred with the Pentamerida, the Orthida diversities declined markedly again in the Přídolí (to 20 genera [11%]). Throughout the Silurian the diversity of the Athyridida remained fairly constant (Fig. 1921).

Reconstructions of Silurian climates indicate that the system was characterized by a gradual warming following the Hirnantian ice age, punctuated by short periods during which continental ice sheets returned (Frakes, Francis, & Sykes, 1992; Grahn & Caputo, 1992). Such an interpretation is consistent with measured $\delta^{18}O$ ratios that show an overall trend toward lower values (implying warming or less glaciation) interspersed with shorter periods of more pronounced oxygen isotope variation (Azmy & others, 1999; Veizer & others, 1999). Strontium isotope ratios also increased gradually throughout the Silurian, and again, this is thought to be a reflection of increasing input of terrestrial sediments as erosion rates and subsequent river transportation of sediments increased as the climate warmed. There are a number of short duration excursions in the $\delta^{18}O$ record, some of which have been interpreted as the result of the periodic development of continental ice sheets during the Silurian (Caputo, 1998), although some other $\delta^{18}O$ excursions (such as determined from the late Homerian and Ludfordian) are not accompanied by any evidence of ice growth and have been attributed to other types of climatic shifts (such as from humid to more arid; Samtleben & others, 1996; Samtleben, Munnecke, & Bickert, 2000). Whatever the nature and duration of these climatic changes, they did not have major effects on overall brachiopod diversity, although factors related to changing climates such as facies changes may well have had an influence on the changing relative dominance of different brachiopod orders during the Silurian.

At the resolution of the stratigraphic data presented here, the Orthida were the dominant order in the aftermath of the major environmental perturbations caused by the Hirnantian glaciation. Although their numbers declined by more than half across the Ordovician Silurian boundary,

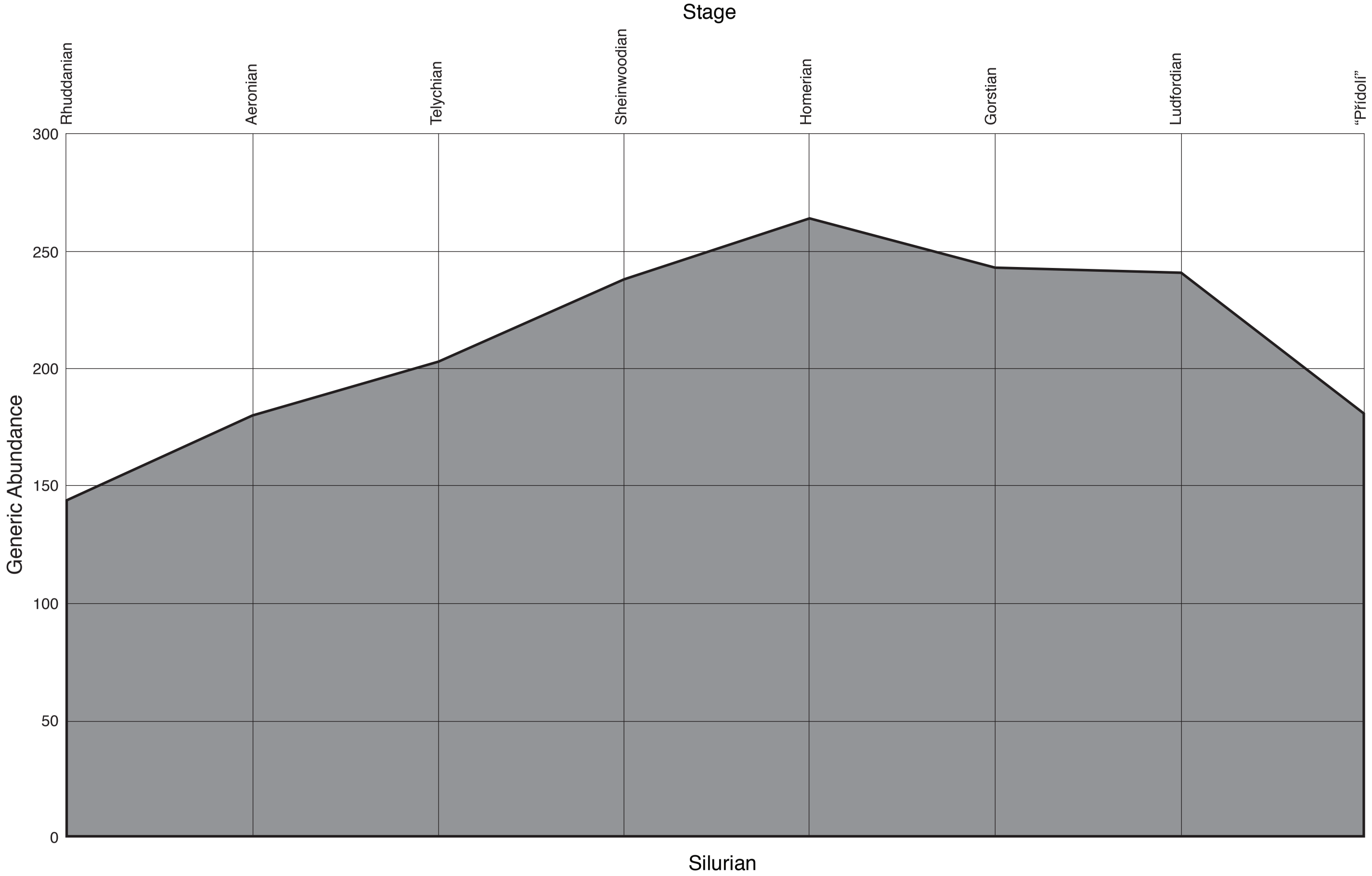

FIG. 1920. Abundance of brachiopods in each of 8 stages (horizontal axis) assigned to the Silurian System, with lowermost stage (Rhuddanian) on left-hand side of horizontal axis and uppermost Přídolí Stage on right-hand side. See Table 40 for stage nomenclature, common abbreviations, meaning of quotation marks, and absolute ages (midpoint, base, and duration) (new).

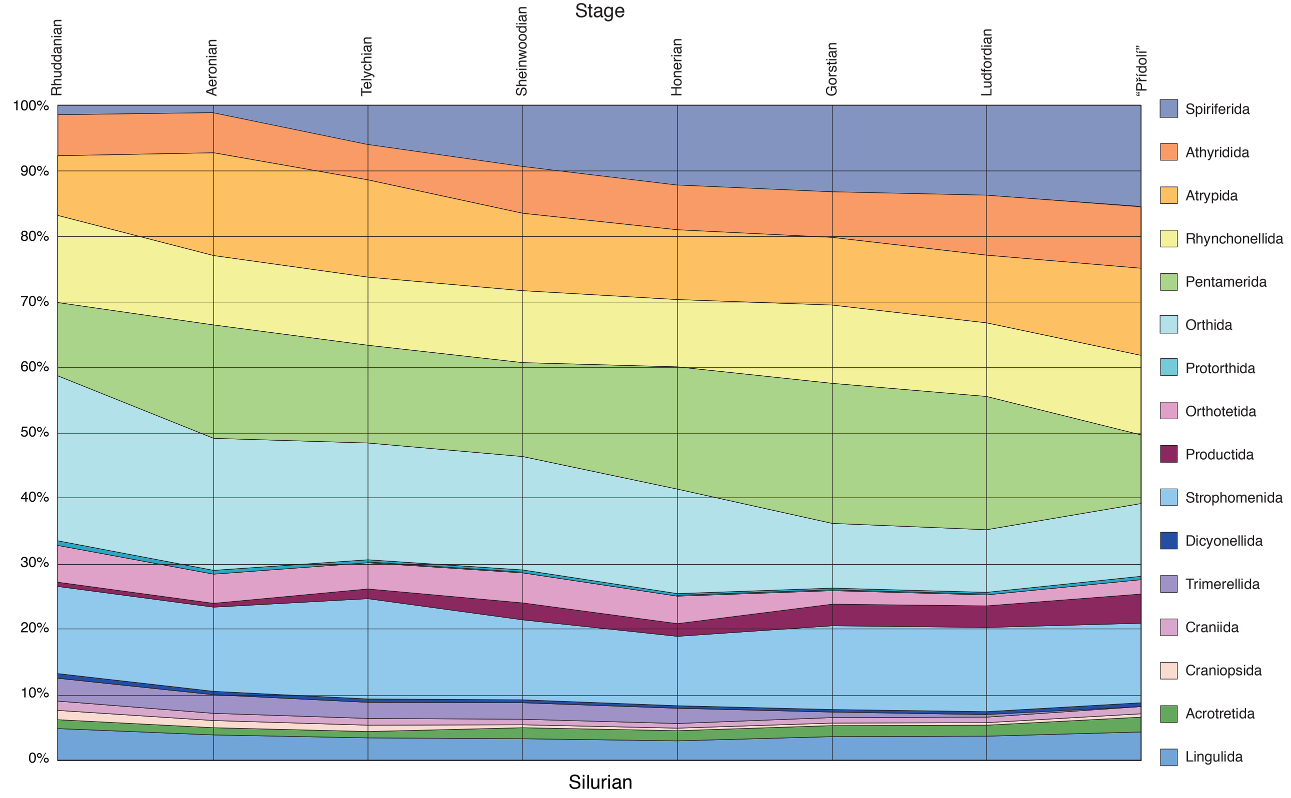

FIG. 1921. Relative proportions of different orders of brachiopod recorded from each of 8 stages of the Silurian System, with lowermost stage (Rhuddanian) on left-hand side of horizontal axis and uppermost stage (Přídolí) on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present; see Table 40 for meaning of quotation marks (new).

they remained the dominant order in the Rhuddanian, but this dominance subsequently declined as the Pentamerida and the Spiriferida became proportionately more significant constituents of the Homerian, Gorstian, and Ludfordian faunas (Fig. 1921). The observed pattern of brachiopod diversity may well be influenced by the evolution of novel and advantageous morphological characters, allowing brachiopods to exploit a wider range of habitats, a phenomenon that will be explored in more detail in the section below dealing with Carboniferous brachiopod diversity.

DEVONIAN SYSTEM

The Devonian System (416.0 ± 2.8 Ma to 359.2 ± 2.5 Ma; Gradstein, Ogg, & Smith, 2004) witnessed two of the most dramatic diversity changes in brachiopod history. Indeed, the most distinctive feature of the system is the fact that not only did the phylum achieve its greatest diversity during the Devonian, but within the system it also suffered one of its greatest declines, second only to that experienced during the mass extinction at the end of the Permian System. These events during the Devonian are unique in brachiopod history, not just in terms of their magnitude, but also because of their stratigraphic and temporal proximity.

Brachiopod diversity increased dramatically during the Lower Devonian, with 266 genera recorded from the Lochkovian Stage, 339 genera from the Pragian Stage, and 460 genera from the Emsian Stage. The latter uppermost Lower Devonian stage records a higher number of brachiopod genera in a single stage than occurs at any other interval of their entire geologic history. In the Middle Devonian the number of brachiopod genera declined significantly and progressively (to 336 genera in the Eifelian and 273 genera in the Givetian), and this trend was continued in the Upper Devonian System, with 206 genera being recorded in the Frasnian and 203 genera in the uppermost Upper Devonian Famennian Stage. Thus, the Devonian System witnessed the greatest recorded diversity of brachiopods, and yet there were fewer brachiopods present at the end of the system than had been present at its beginning (Fig. 1922).

It is also remarkable that the taxonomic diversity of brachiopods, at least at the level of order, changed very little during the expansion and decline of brachiopod diversity during the Devonian. A total of 17 orders are recorded from the entire Devonian System (Fig. 1923), and all 17 of these are present throughout the Lochkovian Stage, the Pragian Stage, and the Emsian Stage. Moreover, they are present in much the same proportions, so the dramatic rise in brachiopod diversity reflects the relative success of a range of orders. Particularly successful, and at least doubling their diversities, were the Strophomenida (increasing from 29 genera in the Lochkovian Stage to 37 in the Pragian Stage and 60 in the Emsian Stage), the Productida (14 genera in the Lochkovian Stage, 31 in the Pragian Stage, 43 in the Emsian Stage), the Spiriferida (40 in the Lochkovian Stage, 70 in the Pragian Stage, 102 in the Emsian Stage), and the Terebratulida (11 in the Lochkovian Stage, 12 in the Pragian Stage, 27 in the Emsian Stage). The Rhynchonellida recorded more modest but still significant proportional increases during the same stages (46 in the Lochkovian, 55 in the Pragian, and 67 in the Emsian). Rhynchonellida genera display an interesting distribution, with a pronounced double peak, each of which involves over 60 genera (a greater number of Rhynchonellida than is present during the Jurassic (a system in which the order achieved a maximum diversity, in any one stage, of 48 genera). Among major groups of brachiopods, only the Orthida failed to capitalize on the rapid expansion of the brachiopods in the Lower Devonian System, and their generic diversities (29 genera in the Lochkovian Stage, 32 in the Pragian Stage, 28 in the Emsian Stage) remained essentially constant during the dramatic rise in the number of genera that culminated during the Emsian Stage.

Thus, the proportions of brachiopod orders remained relatively constant during the Lower Devonian (Fig. 1923). Even in the Middle Devonian, as generic numbers declined, the proportions of the various orders remained fairly constant, marked only by the slight decline of the Pentamerida and Orthida in the Givetian Stage (Fig. 1923) and the increasing proportion of Terebratulida. The Upper Devonian witnessed much greater taxonomic change, with the continuing decline and eventual disappearance of the Pentamerida by the Famennian Stage. The Atrypida, a significant component of brachiopod faunas throughout much of the Devonian System, similarly disappeared at the end of the Frasnian Stage, while the relative contribution of the Strophomenida was greatly reduced during this stage. Several orders that had been present in small numbers also disappeared (the Acrotretida and Protorthida), while the Dictyonellida are only recorded in the Lower Devonian and are not recorded in the Middle or Upper Devonian (although representatives are present in the Lower Carboniferous).

During the Famennian Stage, the relative proportion of nonchonetidine Productida and Spiriferida increased dramatically (Fig. 1923). Despite the fact that the overall number of brachiopod genera decreased significantly, the Productida actually achieved their greatest Devonian diversity during the Famennian Stage (47 genera as compared to 43 during the Emsian Stage), as did the Rhynchonellida with 71 genera from the order being recorded during the Famennian Stage, compared with 67 genera in the Emsian Stage. By contrast, the number of genera of the other major groups of brachiopods present in the Famennian Stage, the Spiriferida had been greatly reduced from their Emsian maximum (42 genera, as compared to 102 genera during the Emsian Stage). The pattern of Terebratulida diversity is also of interest. Having achieved a total of 27 genera in the Emsian Stage, the order achieved a peak of Devonian diversity in the Givetian Stage (33 genera, representing 13% of brachiopods recorded from this stage) before declining drastically to 7 and 3 genera in the Frasnian and Famennian Stages respectively (Fig. 1923).

The Upper Devonian in particular witnessed therefore not only a major reduction of brachiopod genera but also major changes in the relative proportion of different brachiopod groups. Brachiopod faunas at the end of the Devonian were dominated by the Rhynchonellida (35% of the total brachiopod diversity), the Spiriferida (24% of the total), and the Productida (23% of the total, including the Chonetidina as an important suborder at this time). By the end of the system, the number of orders had been reduced to 12.

The Strophomenida is represented in the Devonian Period by both constituent superfamilies, but the Plectambonitoidea died out in the Eifelian, and the Strophomenoidea suffered a major drop in numbers toward the end of the Devonian. The Lower Devonian saw the introduction of two suborders, the Productidina and the Strophalosiidina, which increased in diversity throughout the Devonian System, while the suborder Chonetidina achieved its greatest diversity in terms of the number of genera recorded (39 in the Emsian Stage). In the Famennian, the Protorthida, Pentamerida, and Atrypida died out. The Spiriferinida first appeared near the base of the system, while the Silurian distribution of the Spiriferida reveals a major peak of diversity of 102 genera. The Athyridida continued to increase in numbers from their Silurian high of 22 genera to reach 46 genera by the Emsian Stage, although they declined slightly by the Upper Devonian (Fig. 1921). The Middle Devonian Emsian and Eifelian strata in many places yield well-preserved and readily extractable fossils, so there are well-documented brachiopod faunas from these times when brachiopods were clearly abundant.

The overall pattern of brachiopod diversity during the Devonian has several intriguing aspects. The more rapid diversity

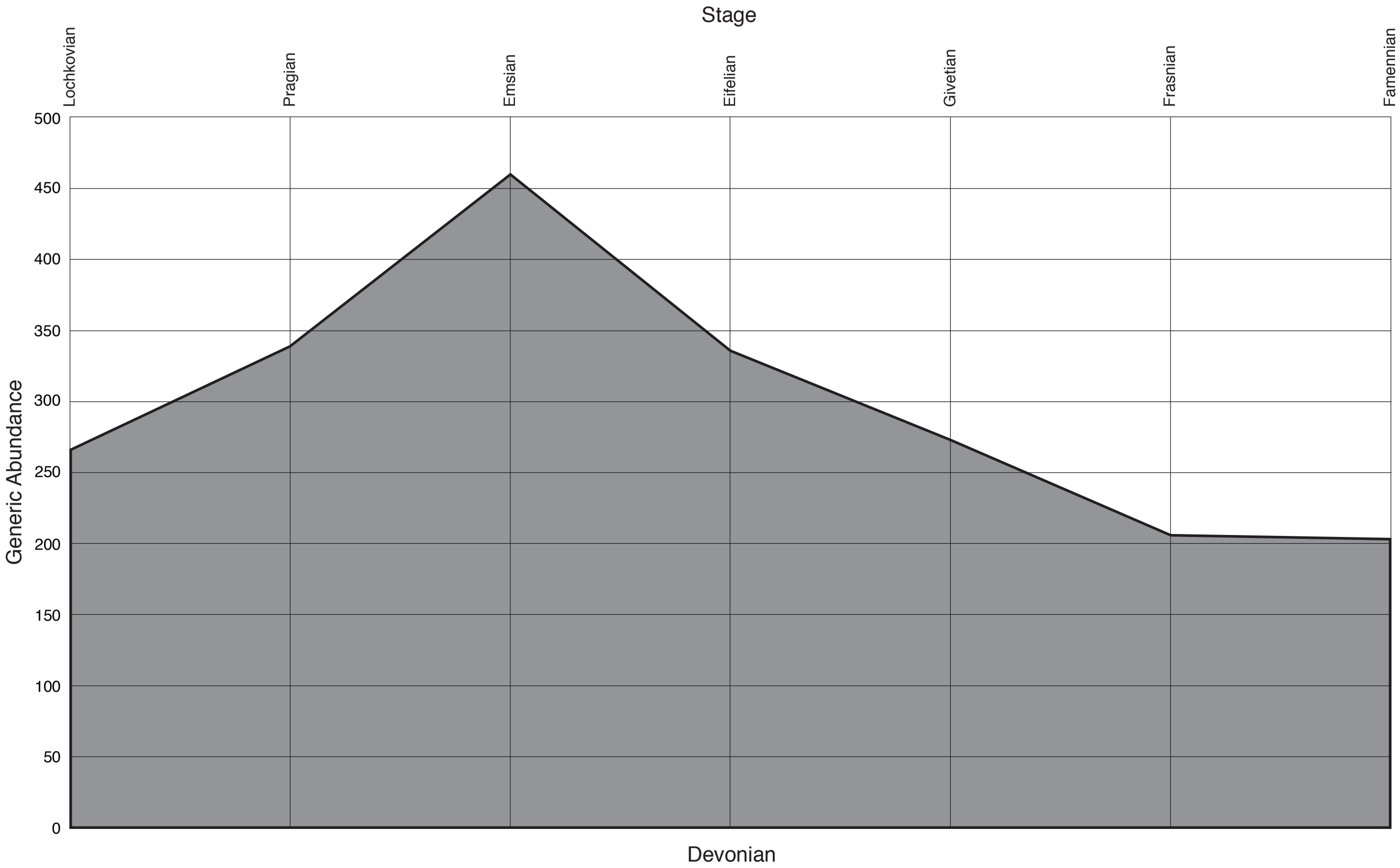

FIG. 1922. Abundance of brachiopods in each of 7 stages (horizontal axis) assigned to the Devonian System, with lowermost stage (Lochkovian) on left-hand side of horizontal axis and uppermost Famennian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

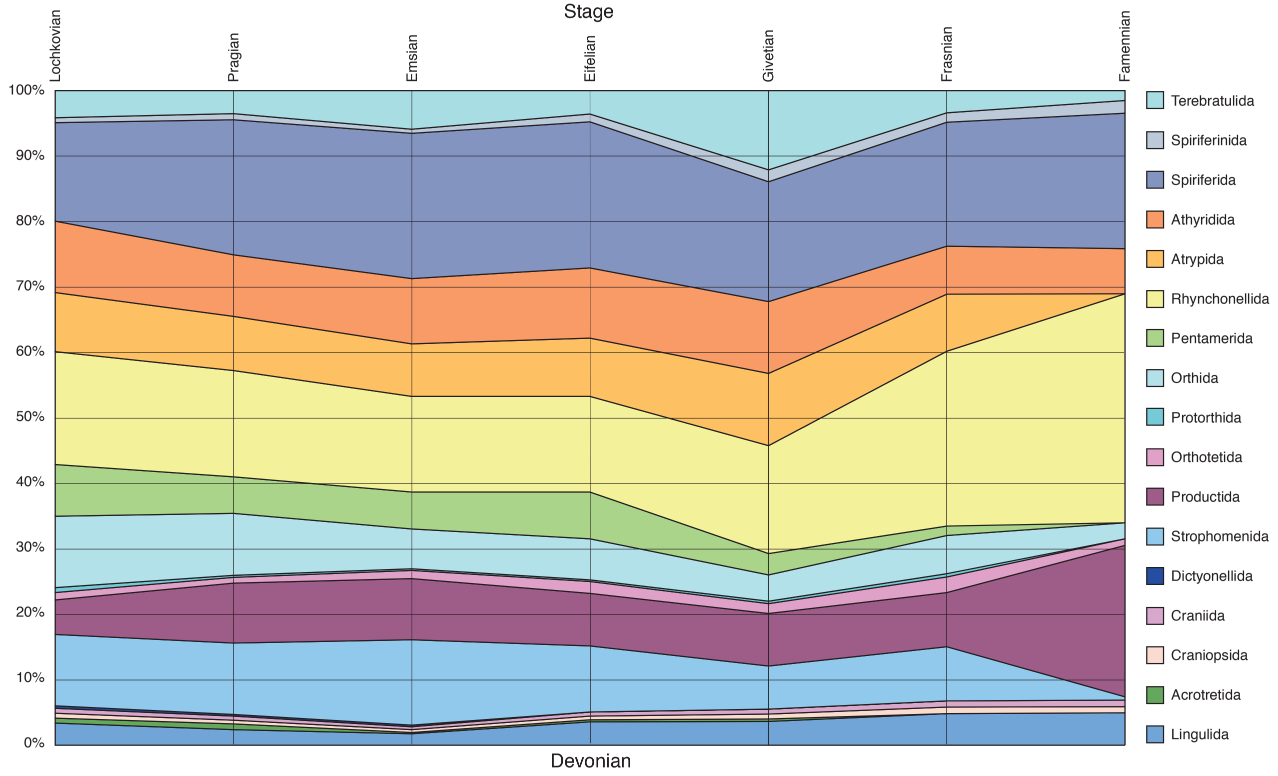

FIG. 1923. Relative proportions of different orders of brachiopods recorded from each of 8 stages of the Devonian System, with lowermost stage (Lochkovian) on left-hand side of horizontal axis and uppermost Famennian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present. Some orders recorded in such low numbers that they are difficult to distinguish in diagram (for example, Protorthida, Dictyonellida, Craniida, Craniopsida, and Acrotretida) but are included in diagram to ensure completeness (new).

increase in brachiopod history was due to increasing numbers of the great majority of dominant groups present at the beginning of the system. This diversification event occurred during a period in the history of the Earth that was marked by a series of marine transgressions and regressions. The indications are that brachiopods flourished in the shallow marine habitats that were created during intervals dominated by marine transgressions and that diversities were not noticeably affected, in this analysis, during periods of regression. Of the major brachiopod groups at the time, only the orthids failed to flourish during the Lower Devonian, perhaps indicating that other stocks possessed some competitive edges in terms of ecological adaptation or habitat colonization.

The decline in brachiopod diversity in the Middle and Upper Devonian is equally intriguing. The Devonian did experience fluctuations in the carbon, oxygen, and strontium isotope curves (HAYES, STRAUSS, & KAUFMAN, 1999; VEIZER & others, 1999). These geochemical indicators of significant environmental perturbation do not, however, appear to provide a ready explanation for the decrease in brachiopod diversity. If the oxygen isotope measurements are considered purely as a valid temperature proxy, then oceanic temperatures were somewhat lower during the Middle Devonian than in the Lower Devonian, but they then suggest that global oceanic temperatures warmed again in the Upper Devonian and were similar to those of the Lower Devonian. There were, however, a number of glaciation events during the Upper Devonian.

The Upper Devonian Frasnian to Famennian event has been considered to be the fifth largest extinction event during the Phanerozoic, although a recent reappraisal has suggested that the Givetian Stage, the Frasnian Stage, and the Famennian Stage all had elevated rates of extinction (HOUSE, 2002). If the patterns observed in the brachiopod stratigraphic charts are real, then it does seem that many representatives of the phylum were initially able to exploit favorable conditions in the Lower Devonian but were then drastically reduced in diversity during the Middle and Upper Devonian. HOUSE (2002) noted that there are numerous extinction events during the Devonian and that many of those in the Middle and Upper Devonian in particular are short-term, clearly defined events related to transgressive-regressive cycles, which are marked by the development of anoxic sediments. The timing of such events (in some cases several occur within a single stage) may be related to Milankovitch cyclicity, in the absence of evidence for volcanic or tectonic influences (HOUSE, 2002).

It may also be that the dramatic patterns of brachiopod diversity in the Devonian reflect the existence of good exposures of particularly richly fossiliferous Devonian strata or the culminations of many years of concentrated activity by brachiopodologists on this system. Alternatively, evolutionary innovation at a level below the orders discussed here might help explain the observed patterns: morphological features that may initially have allowed brachiopods to exploit the Devonian seas but were then too specialized to survive the numerous environmental perturbations (such as the development of anoxic events). HOUSE (2002) stressed that the various Devonian extinction events are related to different phases of transgression-regression cycles and probably have multiple causes. Whatever the cause, it is clear that the Devonian System warrants detailed investigation.

CARBONIFEROUS SYSTEM

At the start of the Carboniferous System (359.2 ± 2.5 Ma to 299.0 ± 0.8 Ma; GRADSTEIN, OGG, & SMITH, 2004), there were 13 orders of Brachiopoda, the 12 present in the uppermost Upper Devonian and the Dictyonellida, a few representatives of which had reappeared after the order was absent from the Middle and Upper Devonian (Fig. 1924). The system was dominated by two of the three orders that had been the major

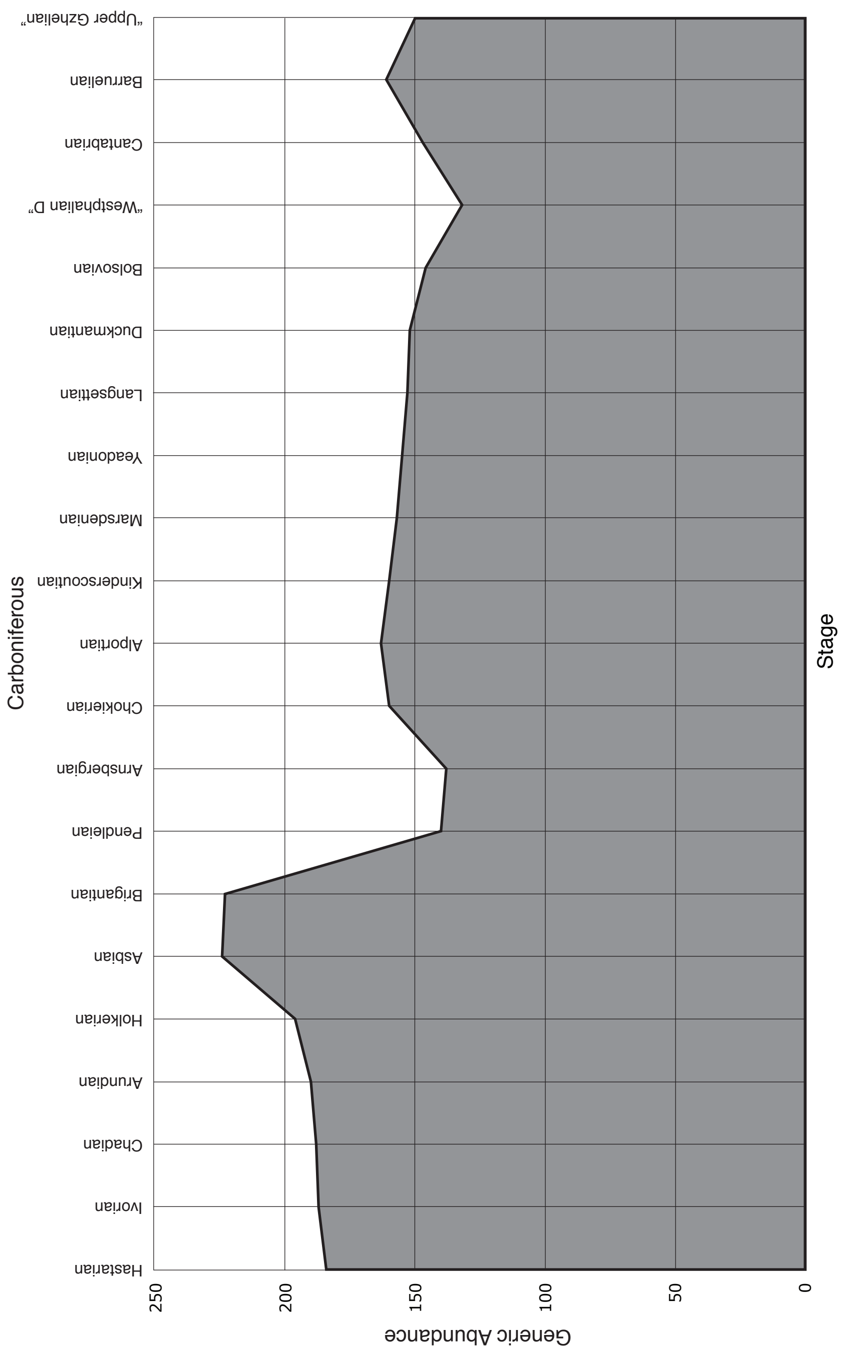

Fig. 1924. Abundance of brachiopods in each of 21 stages (horizontal axis) assigned to Carboniferous System, with lowermost stage (Hastarian) on left-hand side of horizontal axis and uppermost upper Gzhelian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present; see Table 40 for meaning of quotation marks (new).

contributors to brachiopod faunas in the Upper Devonian, namely the Productida (34% of the total number of genera recorded from the entire system) and the Spiriferida (22% of the total number of genera recorded from the Carboniferous). The dominance of the Productida contained representatives of all three constituent suborders (the Productidina, Strophalosiidina, and Chonetidina). All three of these productid suborders waned during the Upper Carboniferous but then increased in generic diversity again during the Gzhelian Stage.

The other dominant order in the Upper Devonian, the Rhynchonellida, declined in numbers drastically at the beginning of the Carboniferous (to represent 16% of the brachiopod fauna in the Hastarian Stage) and declined even further subsequently in the Carboniferous (see Fig. 1926).

The Lingulida and Craniopsida (which died out early in the Carboniferous System), Craniida (with a break in its occurrences in the Upper Carboniferous), and Dictyonellida make up only about 5% of the total brachiopod generic diversity throughout the system (Fig. 1926). In this analysis, the Craniida display the most patchy distribution of any brachiopod order, not only being absent in the great majority of stages in the Upper Carboniferous System (only recorded in the Alportian Stage out of the 12 stages in the Upper Carboniferous), but also lacking any representatives in the Upper Permian System, the entire Triassic System, and being absent from the Lower and Middle Jurassic System (Fig. 1925). Throughout its geologic history the number of Craniida genera has remained very low, reaching a maximum of 5 genera in the uppermost Maastrichtian Stage of the Cretaceous. Taken together, the Terebratulida, Orthida, Spiriferinida, Athyridida, Orthotetida, and Rhynchonellida make up about 39% of the total brachiopods recorded from the Carboniferous System.

During the Carboniferous System the Strophomenida was represented by only a single genus, and the order died out by the Duckmantian Stage. The number of Orthida genera remained almost constant throughout the Carboniferous System, while the Rhynchonellida display a rapid drop from their high in the Devonian and thereafter stabilized in terms of diversity at a plateau of 13 to 16 genera, including 4 endopunctate genera that survived from the Upper Devonian right through to the Upper Permian. The Athyridida show a slow decline throughout the Carboniferous System, with 21 genera in the lowermost Hastarian Stage and only 7 genera by the uppermost upper Gzhelian Stage (Fig. 1926).

In terms of absolute abundances, the generic abundances for the Carboniferous were much lower and much more constant (Fig. 1924) than those for the Devonian, possibly influenced by the fact that the system had been closely subdivided into 21 stages. The overall data show a gradual increase from 184 genera in the lowermost Hastarian Stage of the Carboniferous to a peak of 224 and 223 in the Asbian Stage and the Brigantian Stage respectively (Fig. 1924). This was followed by a sharp decline to 140 and 138 genera, respectively, in the Pendleian Stage and the Arnsbergian Stage, before increasing again, modestly, to remain at 150 to 160 genera for the remainder of the Carboniferous (although the Westphalian D, an unnamed stage in the 1989 IUGS Chart, has only yielded a total of 132 genera).

The initial increase in brachiopod diversity in the Lower Carboniferous can largely be attributed to the success of the Productida, in which the suborder Chonetidina became less abundant, leaving the morphologically diverse true productids to flourish in various environments (Fig. 1926). By the peak of Carboniferous brachiopod diversity, during the Asbian and Brigantian Stages (Fig. 1924, 1926), the Productida had diversified to such an extent that they constituted about half the total brachiopod fauna (in total recording 97 genera out of 224 in the Asbian Stage or 223 in the Brigantian Stage, i.e., 43%). Conversely, by the Chokierian Stage and the Alportian Stage (Fig. 1926), the Productida were still dominant in a fauna that was

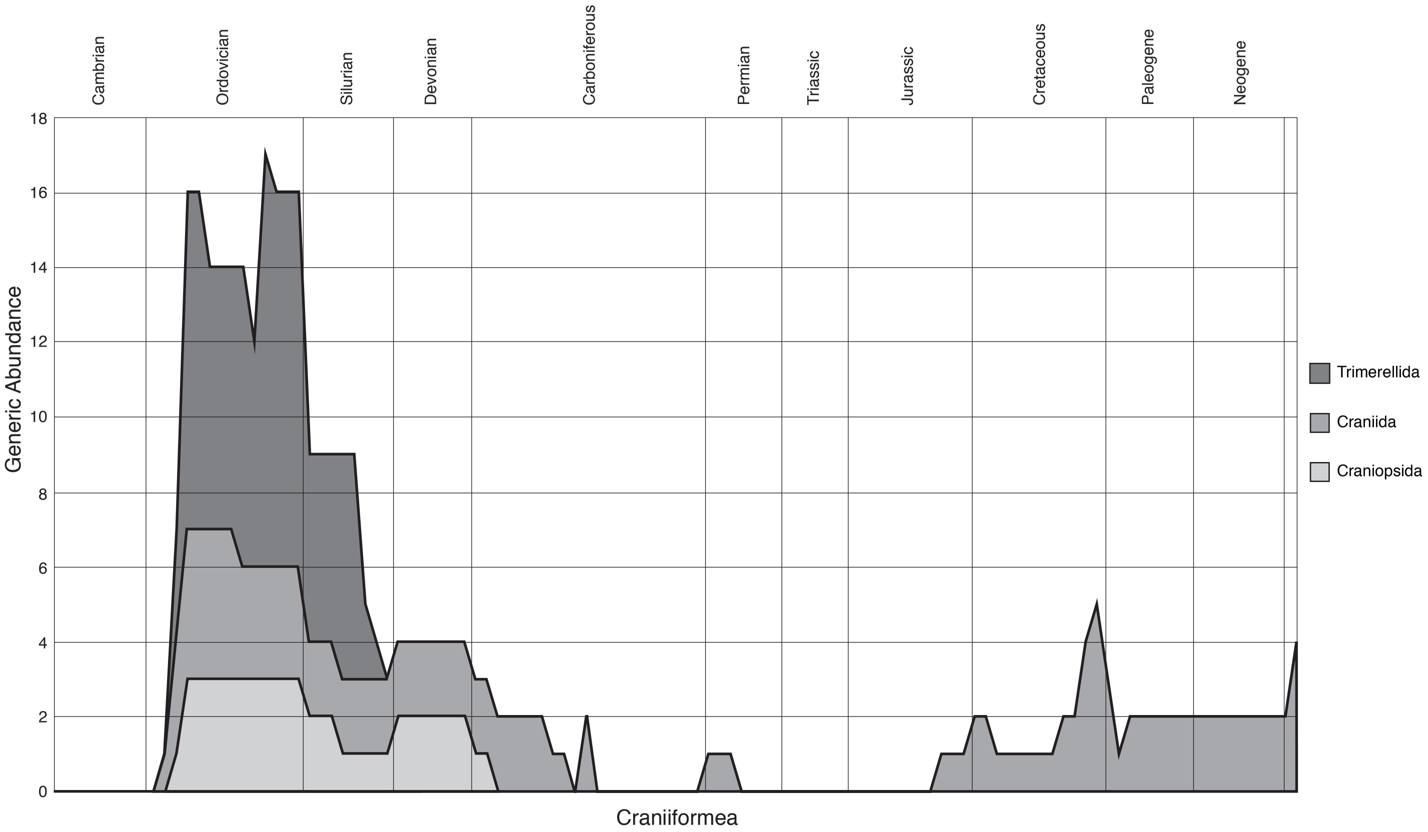

FIG. 1925. Stratigraphic distribution of three orders that comprise subphylum Craniiformea (Trimerellida, Craniida, and Craniopsida). Major gaps are evident in the stratigraphic record of Craniida. Far right, unlabelled segment of diagram portrays distribution in Pleistocene and Holocene stages (new).

considerably reduced in total genera, but the Spiriferida had increased significantly in terms of percentage representation. The total number of Spiriferida genera was virtually identical in the Asbian, Brigantian, Chokierian, and Alportian Stages, but had declined by about a third in the intervening Arnsbergian and Pendleian Stages. This decline is probably linked to the increasingly nonmarine cyclical sedimentation in many areas, leading ultimately to the development of the extensive coal measures that are common throughout the Langsettian Stage to the Westphalian D Stage and obviously led to the disappearance of brachiopods, at least locally.

The differences in diversity and relative proportions may reflect to a certain extent changing sedimentary environments; in Europe at least there is a noticeable change from richly fossiliferous reefal habitats in the Asbian Stage and the Brigantian Stage to more impoverished offshore clastic-dominated environments in the Chokierian and Alportian Stages. From the Chadian Stage to the late Brigantian Stage, warm marine conditions were widespread, with the development of sheet and knoll-like reefs bordering several tectonically controlled blocks. These reefs provided a rich variety of habitats, many of which were exploited by productidines and strophalosiidines, leading to a great variety of morphologies (and taxa) to allow attachment to the varied substrates. Faunas were commonly accessible, readily collected, and, in a few localities, delicately silicified so that paleontologists were able to describe their fossils in detail and great numbers.

The modest peak of 224 genera in the Lower Carboniferous Asbian Stage is surprising in view of the diversity of environments present and the length of time these well-represented rocks have been studied. It seems likely that modern reappraisal of some of these faunas might recognize many more genera than currently listed.

Climate change and associated environmental stress may also have been a factor. The lowermost Lower Carboniferous appears to have been largely ice-free, while subsequently the Carboniferous is characterized by widespread and persistent glaciation, particularly in the southern hemisphere (Mii & others, 2001), during the intervals of Earth history when brachiopod diversity remained low. Rapid shifts in oxygen isotope ratios, including from brachiopod shells (Veizer & others, 1999; Mii & others, 2001) testify to major climatic fluctuations that could well have had a significant influence on brachiopod diversity. Lithologic evidence suggests that glacial and periglacial conditions fluctuated throughout the Early Permian, although there is not universal agreement on this (Dickins, 1996, 2001).

By the end of the Carboniferous System, in the upper Gzhelian Stage, there were 10 orders of extant Brachiopoda. During the Carboniferous the Strophomenida had made their last appearance in the Langsettian Stage, while the Craniopsida barely survived into the Carboniferous and were last recorded in the early Lower Carboniferous Ivorian Stage. As mentioned above, the Craniida have the most disjointed stratigraphic distribution of any brachiopod order (Fig. 1925) and are absent throughout all Upper Carboniferous stages, although they reappear subsequently, and indeed representatives survive to the present day.

PERMIAN SYSTEM

The Permian (299.0 ± 0.8 Ma to 251.0 ± 0.4 Ma; Gradstein, Ogg, & Smith, 2004) is a system of extremes: from ice house to greenhouse, from humid to arid, and from rapid expansion in diversity to one of the largest extinctions recorded in the geologic record. Major excursions in the oxygen, strontium, and carbon isotopic record testify to major environmental perturbations during the Permian (Hayes, Strauss, & Kaufman, 1999; Veizer & others, 1999), yet for much of the system the conditions were conducive for marine life, and brachiopods certainly thrived. Permian reefal facies are present in many parts of the world and appear to

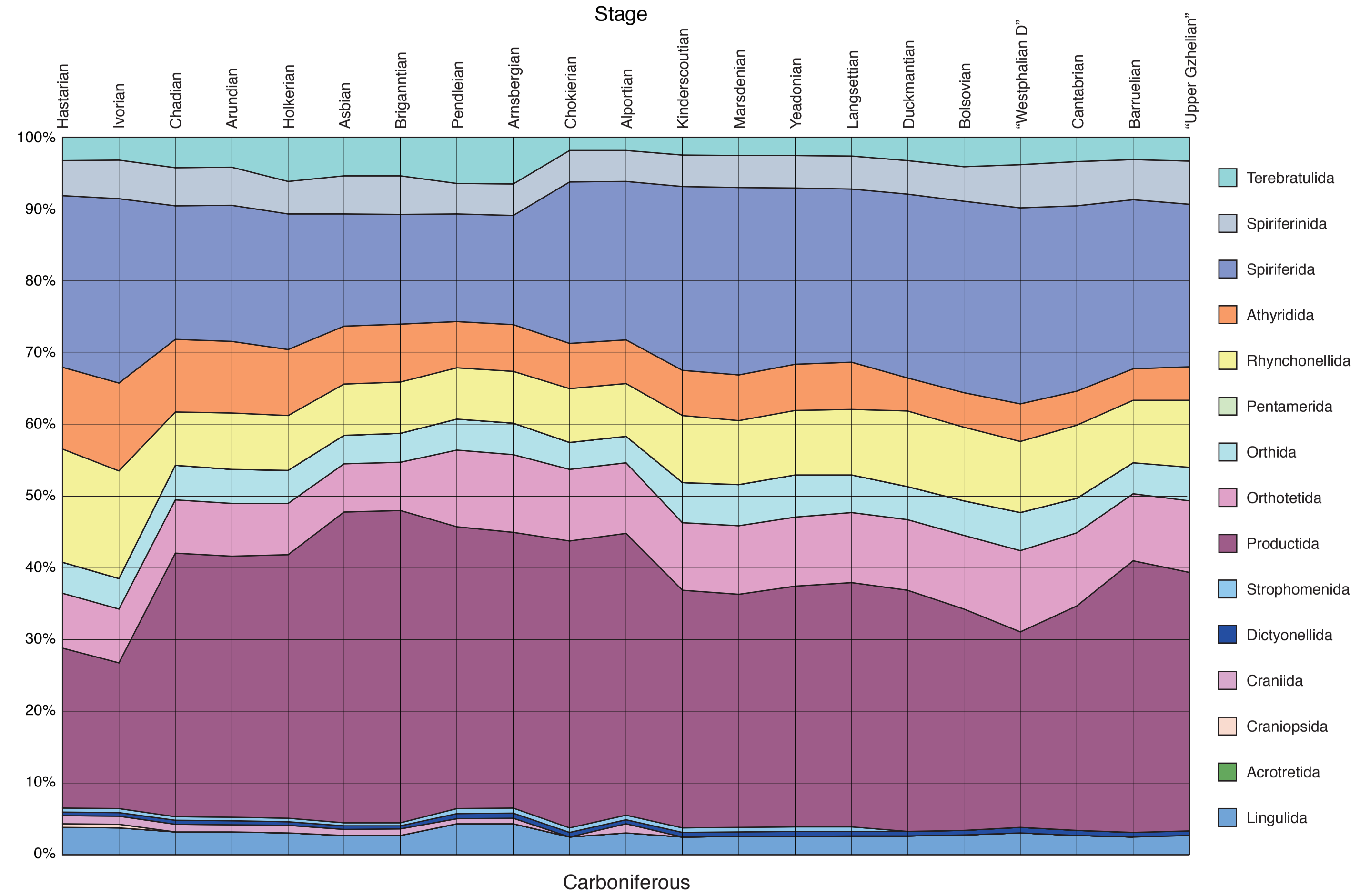

FIG. 1926. Relative proportions of different orders of brachiopod recorded from each of 21 stages of Carboniferous System, with lowermost stage (Hastarian) on left-hand side of horizontal axis and uppermost upper Gzhelian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present; see Table 40 for meaning of quotation marks (new).

have supported diverse brachiopod faunas. Some of the Permian brachiopod fossils are silicified and thus readily extracted almost complete and in large numbers.

Thus, during the Lower Permian, brachiopod diversity climbed steadily to 332 genera in the Roadian Stage, the second highest diversity of brachiopods during their geologic history and more than double the number of genera present throughout most of the Carboniferous Stages. Yet by the end of the Permian System the number of brachiopods was over 100 genera lower than that recorded in the Roadian Stage, the culmination of a decline that started with a very small reduction in the Wordian Stage (to 328 genera), had gathered much greater momentum with the disappearance of 45 genera in the Capitanian Stage (down to 283 genera), and an even more dramatic decline in the Changhsingian Stage (with the disappearance of a further 62 genera to leave a total of 221 genera; Fig. 1927). This was only a precursor to the greatest extinction to affect brachiopods, or indeed many other phyla, as reflected in the number of genera recorded in the succeeding Triassic System (see below).

Representatives of 11 orders are present in the lowermost Asselian Stage of the Permian System, although one of these is the Craniida, which appears impersistently throughout the stratigraphic record and is here only present in the three lowest stages of the Lower Permian. The remaining 10 orders persist throughout the Permian (Fig. 1928). Two of these orders, the Lingulida and the Dictyonellida, are long-ranging groups represented by relatively few genera. The majority of the remaining orders constitute relatively similar proportions of the brachiopod faunas in all seven stages of the Permian, although the Terebratulida increase dramatically in the Upper Permian, contributing a much greater percentage (13%) of the genera in the uppermost Changhsingian Stage of the Upper Permian (up from 5% in the lowermost Asselian Stage of the Permian; Fig. 1928).

The most dramatic feature in the Permian is the major expansion in the numbers of Productida, including the relatively small chonetidine suborder (Fig. 1928). Representatives of the order continue the dominance of brachiopod faunas seen in the Carboniferous, expanding even further during the Permian. 106 genera of Productida were recorded in the lowermost Asselian Stage of the Permian (38% of a total brachiopod fauna of 278 genera; Fig. 1928). By the Roadian Stage of the uppermost Lower Permian, Productida generic numbers had increased to 171 and accounted for 48% of the total brachiopod fauna recovered from this stage (Fig. 1928). Such overwhelming dominance of the faunas continues into the lowermost Upper Permian Wordian Stage (155 genera, equivalent to 50% of a total of 328 genera in this stage). In subsequent stages the number of Productida recorded declines (to 127 genera in the Capitanian Stage and 80 genera in the Changhsingian Stage). Despite this decline in absolute numbers, the Productida remained the dominant order of brachiopods throughout the Permian. In the Changhsingian Stage, for example, the Productida contribute 36% of brachiopod genera, more than double the representation of the two other high-abundance orders (the Spiriferida at 16% and the Terebratulida at 13%; Fig. 1928).

A dramatic change in the taxonomic components of brachiopod faunas occurred between the Roadian and the Changhsingian Stages (Fig. 1928). The reduction in Productida (in both absolute number of genera and percentage of the total number of brachiopods) may reflect a life-style of strong substrate attachment that was more successful in the carbonate-dominated Roadian Stage than in the Changhsingian Stage when clastic deposition was more widespread. Such a phenomenon could also help explain the doubling of the number of Terebratulida genera (to 29 genera [13%] in the Changhsingian Stage from 15 in the Roadian Stage [5%] during a period in which the overall number of brachiopods dropped by a third. The pedunculate lifestyle of the Terebratulida may well be more suitable for clastic-dominated environments, compared to the free-living or closely attached Productida life habit that proved so successful during the Roadian Stage with its firm reefal substrates. SHEN and SHI (1996) discussed the diversification and extinction patterns of Permian brachiopods from southern China.

During the Lower Permian the global climates gradually warmed from the glacial conditions that prevailed during the Upper Carboniferous. It was during these favourable conditions that the Permian expansion in brachiopod diversity occurred. It has been suggested that the peak of brachiopod diversity in the Middle Permian was related to the closing ocean between the converging Indian and Eurasian tectonic plates. As conditions warmed after a colder interval in Earth history, the development of abundant islands and small terranes would have provided numerous ideal environments for brachiopods to proliferate. The absolute peak in brachiopod diversity in the Roadian Stage actually occurred during an interval of Earth history when the global climates were showing signs of cooling again (i.e., the global oxygen isotope curve; VEIZER & others, 1999), and indeed there is localized evidence of further and very significant cooling after the Roadian Stage (GRADSTEIN, OGG, & SMITH, 2004).

Although there are good grounds for accepting the validity of the Permian for demonstrating the greatest ever brachiopod diversity, there are also indications that this is perhaps the best example of the significant effect that excellent preservation and human effort can have on the recorded stratigraphic distribution of the brachiopods. The rich brachiopod faunas of the reefal lithologies in the Glass Mountains, Texas, United States, have been preserved in superb detail by silicification, which allows them to be extracted from carbonate rocks by dissolution of the matrix using dilute acid. Such preservation should allow a much greater proportion of the fauna to be recovered than is the case with clastic sediments. The descriptions of the Glass Mountain faunas mainly cover the Artinskian to the Wordian Stages, with a peak in the Roadian Stage (and hence closely follows the overall pattern of brachiopod diversity during the Permian System). Here, as in the Lower Carboniferous, the reefal environments supported large proportions of productidines and strophalosiidines, together with richthofeniids and lyttoniids, all of which display an array of morphological adaptations fitting them to their particular habitats. The numbers of genera described by COOPER and GRANT from the Glass Mountains (COOPER & GRANT, 1969, 1974, 1975, 1976a, 1976b) were prodigious. Other Permian brachiopod specialists have contributed many generic names from other geographic areas, adding to the scale of the mid-Permian peak. The question is whether these high diversity numbers are biologically realistic in areas of high productivity, or whether they present a more or less artificial picture of diversity due to the acutely tuned differentiation of morphological features resulting from excellent preservation and intense research work by numerous experts?

PERMO-TRIASSIC EXTINCTION EVENT

The most dramatic event in brachiopod history occurred at the Permian-Triassic boundary. In a global event affecting many other phyla, brachiopod diversity was decimated, literally, by the greatest mass extinction during the Phanerozoic. Only 22 genera are recorded in the lowermost Scythian Stage of the Triassic (Fig. 1929), compared with 221 genera in the uppermost Changhsingian Stage of the Permian System. The situation may be even more dramatic as only 4 of the 22 genera recorded from the Scythian Stage range through from older stages. The remainder presumably evolved during the Scythian (although such a small number may reflect human bias in that investigators may well expect to encounter new genera

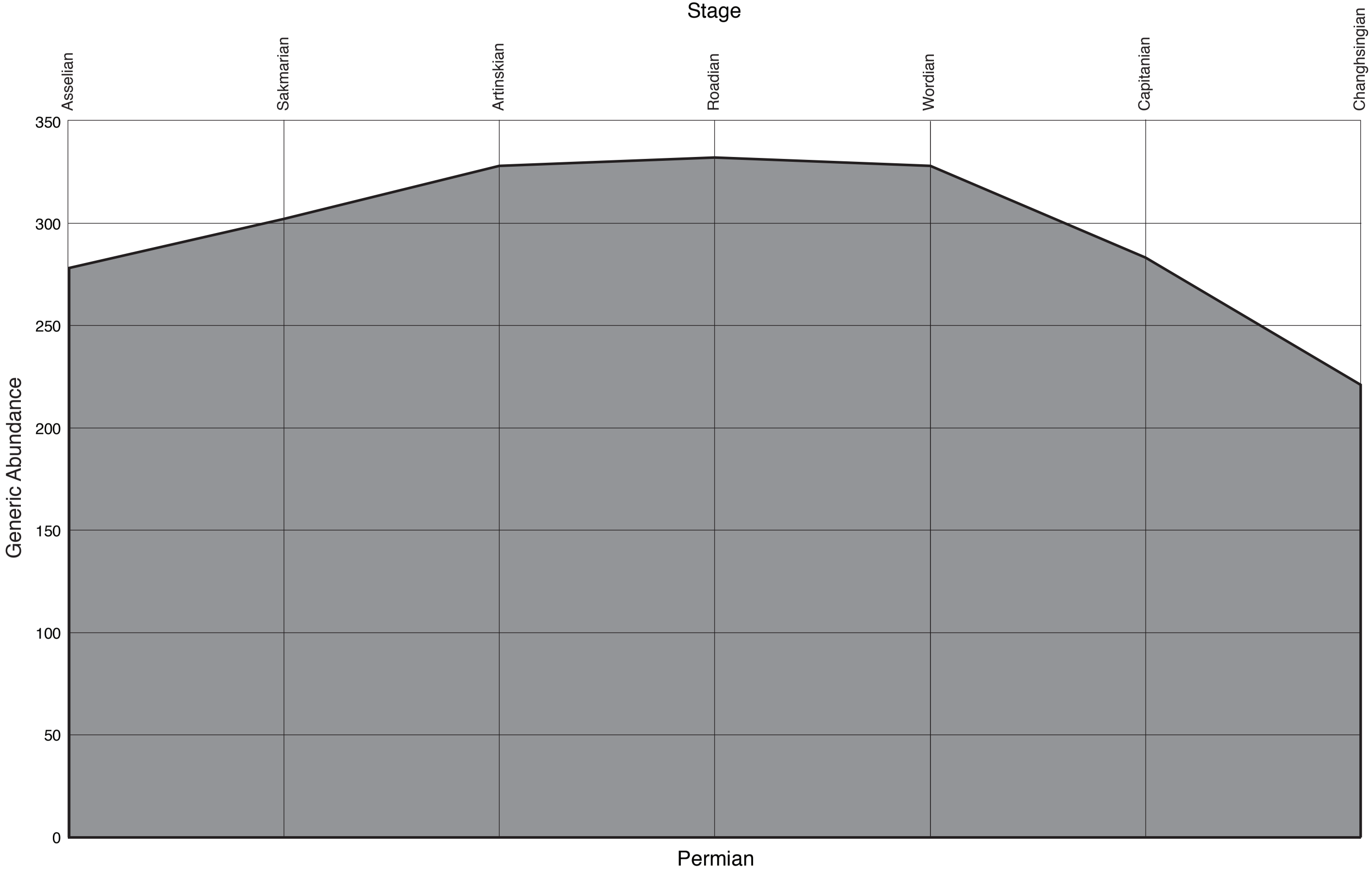

FIG. 1927. Abundance of brachiopods in each of seven stages (horizontal axis) assigned to Permian System, with lowermost stage (Asselian) on left-hand side of horizontal axis and uppermost Changhsingian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

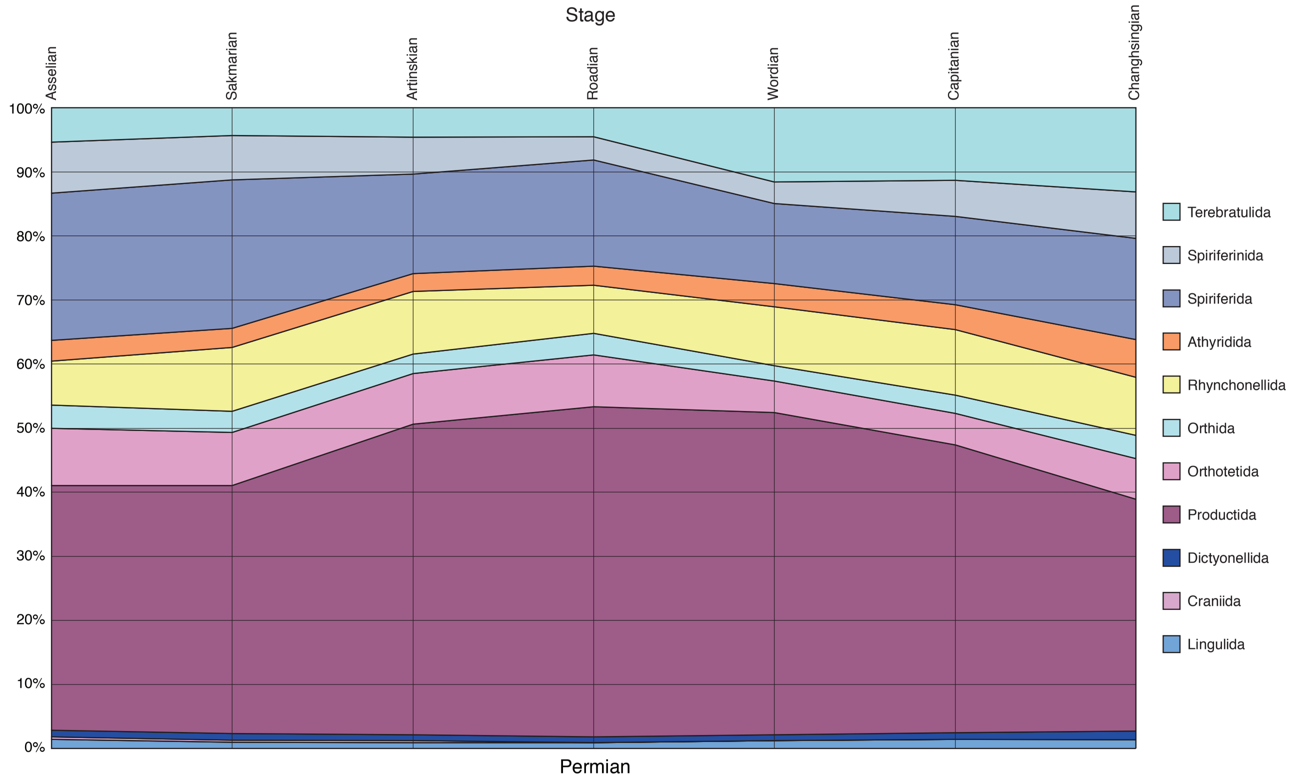

FIG. 1928. Relative proportions of different orders of brachiopod recorded from each of 7 stages of Permian System, with lowermost stage (Asselian) on left-hand side of horizontal axis and uppermost Changhsingian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present. One order (Craniida) is recorded in such low numbers that it is difficult to distinguish but is included in the diagram to ensure completeness (new).

immediately following such a major extinction). Furthermore, 4 genera are only listed as being present in the Triassic and hence may or may not be present in the Scythian Stage. Indeed, recent evidence from SHEN and others (2006) indicates that among the brachiopods only lingulids may have crossed the actual boundary, as it is exposed in northern Italy and southern China. Therefore, during the Scythian Stage there may have been as few as 18 brachiopod genera on Earth, and some of these may have evolved during the 10-million-year extent of the stage as it was defined in the 1989 IUGS Chart (although in the most recent review, the stage had been subdivided into two stages, the Induan Stage and the Olenekian Stage, and the absolute age range of the pre-Anisian Stage Triassic successions has been reduced to approximately 6 million years; GRADSTEIN, OGG, & SMITH, 2004).

If extraordinarily low numbers of brachiopods did survive the transition from the Permian to the Triassic, then the pace of generic reintroduction after the mass extinction must have been rapid. The data presented here suggests that a number of brachiopod orders display continuity through the Permian-Triassic crisis (such as the Athyridida). Furthermore, the Spiriferida increased its generic diversity from the Carboniferous into the Permian and did not die out until the end of the lower Triassic.

The causes of the Permian-Triassic extinction event have been much debated and appear complex (WIGNALL, 2001; ERWIN, BOWRING, & JIN, 2002; SHEN & others, 2006). Current explanations suggest that rapid warming during the Late Permian (possibly associated with the formation of the supercontinent Pangea), interspersed with short intervals of pronounced cooling (due to the eruption of extensive basalts in what is now Siberia), were major controlling factors in the mass extinction. The effects of poorly oxygenated waters spreading over areas of shallow seas, of the type inhabited by brachiopods, has also been implicated (WIGNALL & HALLAM, 1992). Whatever the causes, there is extensive evidence of major environmental change and faunal turnover at the Permian-Triassic boundary, although geochemical evidence suggests that this was only the culmination of severe climatic and biological perturbations that are evident in the Late Permian. There is a major carbon isotope excursion in the Changhsingian Stage, for example, testifying to major changes in the biogeochemical cycling of carbon, which is almost certainly related to the extinction.

Taking the reduction of brachiopod generic abundances at face value may be an oversimplification, however. A high proportion of taxa (up to 50%) that apparently become extinct at the Permian-Triassic boundary reappear later in the stratigraphic record (so-called Lazarus taxa; ERWIN, BOWRING, & JIN, 2002), demonstrating the imperfection of the fossil record and the effects of exposure and taxonomic practice. Certainly, brachiopod diversity does increase subsequently, to 117 genera in the middle Upper Triassic Norian Stage.

Whatever the cause and the true extent of brachiopod mass extinction at the generic level, there is no doubt that the phylum underwent a major decline, one from which it never recovered. Certainly, the brachiopods were never again to dominate global benthic marine communities to the extent that was evident during the Paleozoic. The number of genera recorded in the Scythian Stage is the lowest of any stage in their entire geologic history, and if the *Treatise* data are representative, then there are more than five times the number of genera present in today's oceans, where the phylum has a very low profile. Once again, however, the apparent significant rise in brachiopod generic diversity from the Pleistocene to the present day (Fig. 1912, and discussed below) is almost certainly a clear demonstration of the imperfection of the fossil record, and the concentration of human interest, rather that an indication of a revival of fortune for the phylum.

TRIASSIC SYSTEM

In the Triassic System (251.0 ± 0.4 Ma to 199.6 ± 0.6 Ma; GRADSTEIN, OGG, & SMITH, 2004), four of the ten orders recorded from the uppermost Changhsingian Stage of the Permian System had disappeared, and the Craniida, which have a particularly patchy stratigraphic record (Fig. 1925), were also absent. The four orders that had disappeared were the Orthida, Orthotetida, Dictyonellida, and Productida (although some workers argue that there was a small holdover from the Permian by the Productida [SHEN & others, 2006], but evidence is scant and much appears to depend upon the exact timing of the main extinction episodes as compared to the end of the Permian). These orders represented, respectively, 4%, 6%, 1%, and 36% of the Upper Permian Changhsingian Stage brachiopod faunas. There is a record of 8 productid species surviving into the Triassic, at least in China (SHEN & SHI, 1996), but these records are not present in the *Treatise* data summarized here.

The *Treatise* data indicate that a total of six brachiopod orders are unequivocally represented in the lowermost Scythian Stage of the Triassic System (Fig. 1930), and major taxonomic components of all Mesozoic and subsequent brachiopod faunas have become established. By the beginning of the Triassic System all the major Paleozoic brachiopod orders had disappeared. Although not as numerically significant as the Productida, Orthida, Spiriferida, or Pentamerida, the Rhynchonellida did survive and continue to the present day.

The genera that survived the mass extinction are predominantly the Terebratulida and Rhynchonellida, two orders that, along with the long-lived Lingulida and the inconsistently recorded Craniida, survive to the present day. By the Upper Triassic Carnian Stage, the Thecideida, an order that also survives to the present day in small numbers, had appeared. A further two orders that have no living relatives survived the mass extinction, namely the Spiriferinida and the Athyridida. The Spiriferinida in particular thrived in all post-Scythian Stages of the Triassic System (Fig. 1930). The nonpunctate Athyrididina and the endopunctate Retziidina within the Athyridida died out by the end of the Triassic (in the upper Norian Stage). Only the distinctive koninckinidines have been definitely recorded in the Lower Jurassic. Another order, the Craniida, has been recorded in systems before and after, but not in, the Triassic System (Fig. 1925).

In terms of absolute generic numbers, brachiopods actually staged a modest but sustained recovery during the Triassic, to such an extent that 117 genera were present during the penultimate Norian Stage of the Upper Triassic (Fig. 1929–1930). The faunas of the Norian were dominated by the Rhynchonellida (30 genera: 26% of the total fauna) and the Terebratulida (36 genera: 31%), and these two orders remained dominant throughout the Mesozoic and up to the present day. The Spiriferinida also remained a major contributor to Triassic faunas, accounting for 25% of the genera recorded (29 out of a total of 117 genera recorded from the Norian Stage). The Athyridida were also well represented, with 16 genera in the Norian Stage representing 14% of the fauna. Indeed, combining all stages of the Triassic, the Spiriferinida were the most abundant order (29% of the total fauna), followed in descending order (based on percentage contribution to the total Triassic fauna), by the Terebratulida (25%), Rhynchonellida (24%), and Athyridida (16%; Fig. 1930).

The uppermost Rhaetian Stage of the Triassic witnessed a significant drop in brachiopod diversity, with the total number of genera dropping by 32 (to 85) as

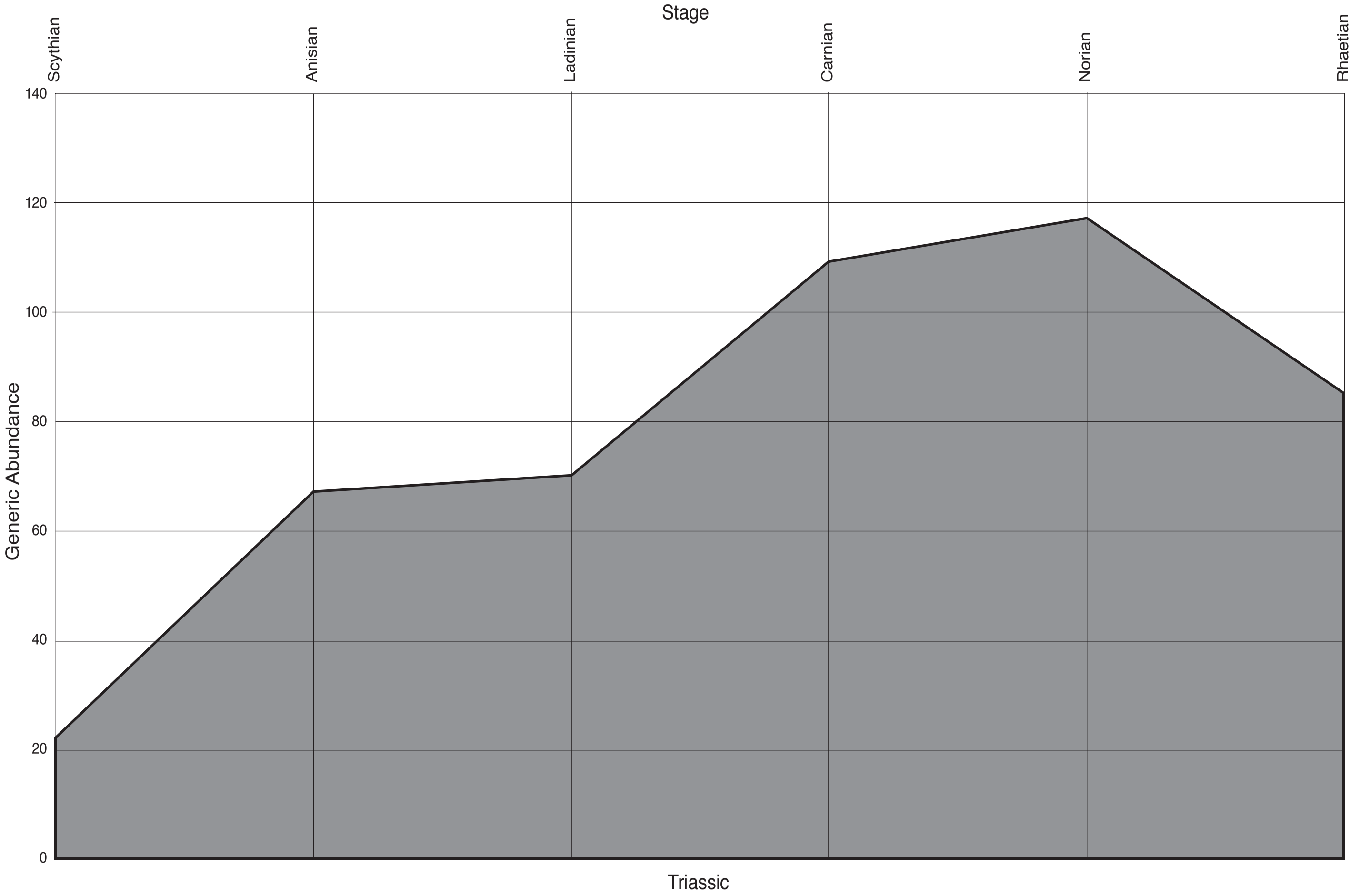

FIG. 1929. Abundance of brachiopods in each of 6 stages (horizontal axis) assigned to Triassic System, with lowermost stage (Scythian) on left-hand side of horizontal axis and uppermost Rhaetian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

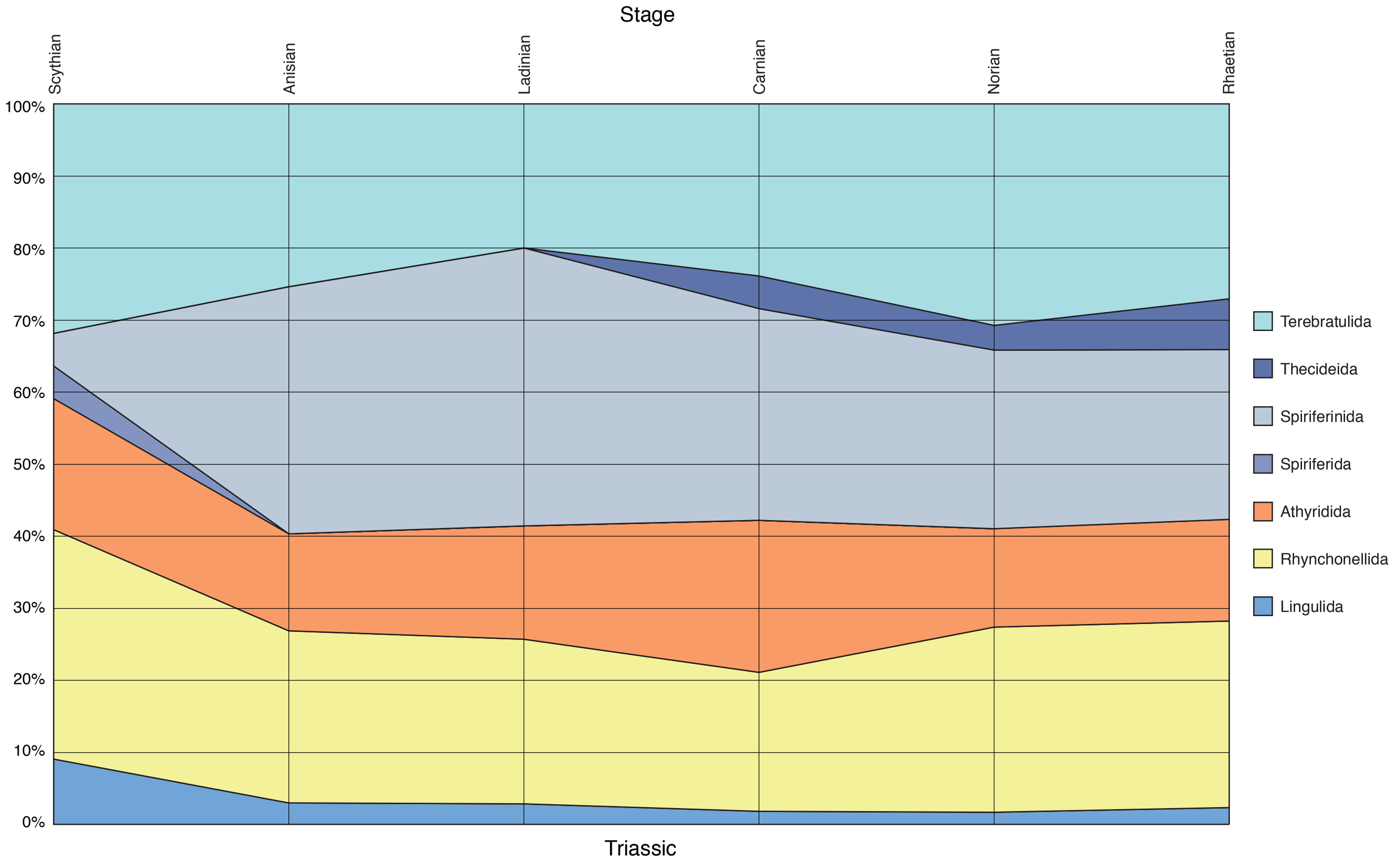

FIG. 1930. Relative proportions of different orders of brachiopods recorded from each of 6 stages of Triassic System, with lowermost stage (Scythian) on left-hand side of horizontal axis and uppermost Rhaetian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present (new).

compared with the preceding Norian Stage. This reduction affected all major groups of Triassic Brachiopoda: the Terebratulida (down to 23 in the Rhaetian Stage from 36 in the Norian Stage), Rhynchonellida (down to 22 in the Rhaetian Stage from 30 in the Norian Stage), Spiriferinida (down to 20 in the Rhaetian Stage from 29 in the Norian Stage), and Athyridida (down to 12 in the Rhaetian Stage from 16 in the Norian Stage). By contrast, the recently evolved Thecideida showed an increase from 4 genera in the Norian Stage to 6 in the Rhaetian Stage. The Lingulida are represented by two genera in all Triassic stages. In terms of percentages, most groups of brachiopods were affected equally by the decline in the Rhaetian Stage, with perhaps the Terebratulida being the most strongly affected (down to 27% of the fauna in the Rhaetian Stage from 31% of the fauna in the Norian Stage).

This apparent decline is not accompanied by any known geochemical perturbation that might indicate some environmental shift that could have had a negative impact on brachiopod diversities in the Rhaetian Stage. Indeed, this apparent decline could well demonstrate an artefact of the stratigraphic process. In the 1989 stratigraphic chart, the Rhaetian Stage was considered to have an absolute age range from around 210 to 205 Ma, in effect lasting for 5 million years, while the Norian Stage represented 10 million years of geologic history (220 to 210 Ma). This discrepancy is even greater in the most recent revision of the geologic time scale (GRADSTEIN, OGG, & SMITH, 2004), in which the absolute range of the Norian Stage is extended to 13 million years (from 216.5 Ma to 203.5 Ma), while that of the Rhaetian Stage has been reduced to approximately 4 million years (203.5 to 199.6 Ma). The Norian Stage has a duration that is comparable to that of all other Triassic stages, suggesting that the steady increase in brachiopod generic abundance up to the Norian Stage probably does reflect a genuine progressive recovery of the phylum from the Permo-Triassic mass extinction. The abnormally short duration of the Rhaetian Stage, however, may be a contributing factor in the apparent decline in generic diversity recorded in this stage. The succeeding Hettangian Stage of the Jurassic, in common with many Jurassic stages, also has a relatively short absolute time range (Table 40). A total of 26 genera recorded from the Hettangian Stage appear for the first time in this basal Jurassic stage, compared with only 14 that range through from the uppermost Triassic Rhaetian Stage. Therefore, if the two stages were combined into a single stratigraphic entity, approximately comparable in duration to the preceding Triassic stages (9 million years as compared with 10 million years for the Norian and Carnian Stages), then the total number of genera recorded would be 111 (as compared with 112 in the Norian Stage and 106 in the Carnian Stage). There is nevertheless a sustained decline in brachiopod diversity in post-Hettangian Stages during the Lower Jurassic, and it was not until the Middle Jurassic that the total number of genera achieved levels comparable to those that prevailed during most of the Upper Triassic (see below).

JURASSIC SYSTEM

In the Jurassic System (199.6 ± 0.6 Ma to 145.5 ± 4.0 Ma; GRADSTEIN, OGG, & SMITH, 2004), the four stages of the lower series saw brachiopod diversities reach a maximum of 84 genera in the Pliensbachian Stage, having increased from 46 genera in the Hettangian Stage, and 65 genera in the Sinemurian Stage. During the uppermost Toarcian Stage of the Lower Jurassic, the number of genera declined slightly to 75 genera (Fig. 1931). This level of diversity was sustained in the lowermost Aalenian Stage of the Middle Jurassic (with 75 genera), increased to 109 genera in the Bajocian, and reached a maximum, for the Jurassic, of 114 genera in the Bathonian Stage. The succeeding Callovian Stage, the uppermost Middle Jurassic stage, recorded 105 brachiopod genera. Never again in any younger stage during their subsequent geologic history would there be more than 100 brachiopod genera (with the exception of the Holocene stage, which is anomalous for a paleontological analysis, in that it includes all the taxa described in the present oceans; see below). The three stages of the Upper Jurassic witnessed the onset of the decline, with a steady decrease in brachiopod diversity from 86 genera in the Oxfordian Stage, to 74 genera in the Kimmeridgian Stage, and finally to 67 genera in the Tithonian Stage (the uppermost stage of the Jurassic System; Fig. 1931).

In brachiopod terms, the Jurassic is the age of the Terebratulida and the Rhynchonellida (Fig. 1932). The proportion of Jurassic faunas represented by the Terebratulida increases steadily, from 43% in the lowermost Hettangian Stage of the Jurassic to 67% in the uppermost Tithonian Stage of the Jurassic. The predominance of the Rhynchonellida fluctuates much more, from a low of 25% in the uppermost Upper Jurassic Tithonian Stage and 26% in the lowermost Lower Jurassic Hettangian Stage to a high of 42% of the brachiopod fauna in the Bathonian Stage and 43% in the Aalenian Stage (Fig. 1932). In the Sinemurian Stage, the Rhynchonellida actually contributed a greater percentage of the fauna (26 genera representing 40% of the fauna) than the Terebratulida (25 genera representing 38% of the fauna). By the three stages of the Upper Jurassic however, the Rhynchonellida contribution to the fauna had declined to between 28% and 27% of the brachiopod faunas, with a total of 23 genera in the Oxfordian Stage, 19 genera in the Kimmeridgian, and 17 genera in the uppermost Upper Jurassic Tithonian Stage (Fig. 1932).

The same 6 orders that were present in the Upper Triassic were present throughout the Lower Jurassic (Fig. 1932). The ever-present Lingulida are represented by their customary small number of genera, while the Thecideida, which first evolved in the Triassic System, maintained a consistent presence in all Jurassic stages, although represented by only a few genera (ranging from a maximum of 5 in the Toarcian, Aalenian, and Bajocian Stages to a minimum of 2 in the Kimmeridgian and Tithonian Stages).

The Spiriferinida survived as significant constituents of brachiopod faunas throughout the Lower Jurassic (6 genera in all three stages), but disappear from the geologic record by the lowermost mid-Jurassic Aalenian Stage (Fig. 1932). The Athyridida have a similar history, although represented by only three genera throughout the Lower Jurassic (all included in the suborder Koninckinidina). The last appearance of both orders in the uppermost Lower Jurassic Toarcian Stage therefore coincides with the trough in the distribution curve in the succeeding Aalenian stage (Fig. 1931). The predominance of Terebratulida and Rhynchonellida was therefore well established by the beginning of the Middle Jurassic (Fig. 1932). The increase in the absolute abundance of brachiopods recorded in the Bajocian and Bathonian Stages is almost entirely due to the success of the Terebratulida, which almost doubled in diversity between the Aalenian and the Bajocian Stages (from 35 to 60 genera). Rhynchonellida generic abundances increased only slightly in these stages (32 genera in the Aalenian Stage and 39 in the Bajocian Stage). The impersistent Craniida reappeared in the Upper Jurassic Oxfordian Stage (Fig. 1925) but are represented by only 1 genus throughout the last three stages of the Upper Jurassic. Accordingly, by the end of the Jurassic there were 5 orders present, although the Terebratulida and Rhynchonellida so dominated faunas that together they contributed 92% of the genera recorded from the uppermost Tithonian Stage. These five orders all survive to the present day, in much the same proportions as were evident during the Middle and Upper Jurassic, a period of around 175 million years (GRADSTEIN, OGG, & SMITH, 2004).

For brachiopods, the most dramatic phenomena during the Jurassic were the events during the Toarcian Stage that may

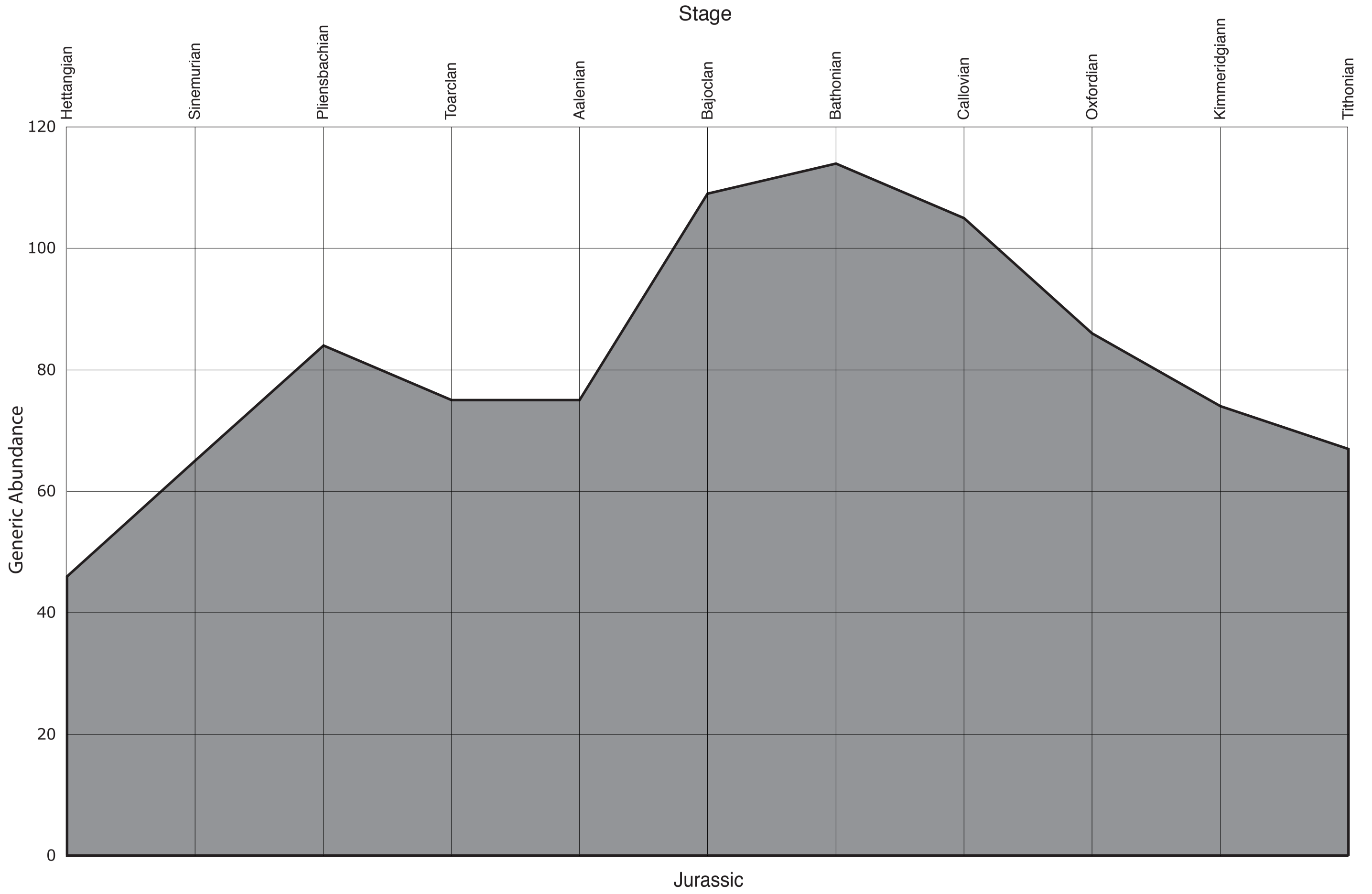

FIG. 1931. Abundance of brachiopods in each of 11 stages (horizontal axis) assigned to Jurassic System, with lowermost stage (Hettangian) on left-hand side of horizontal axis and uppermost Tithonian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

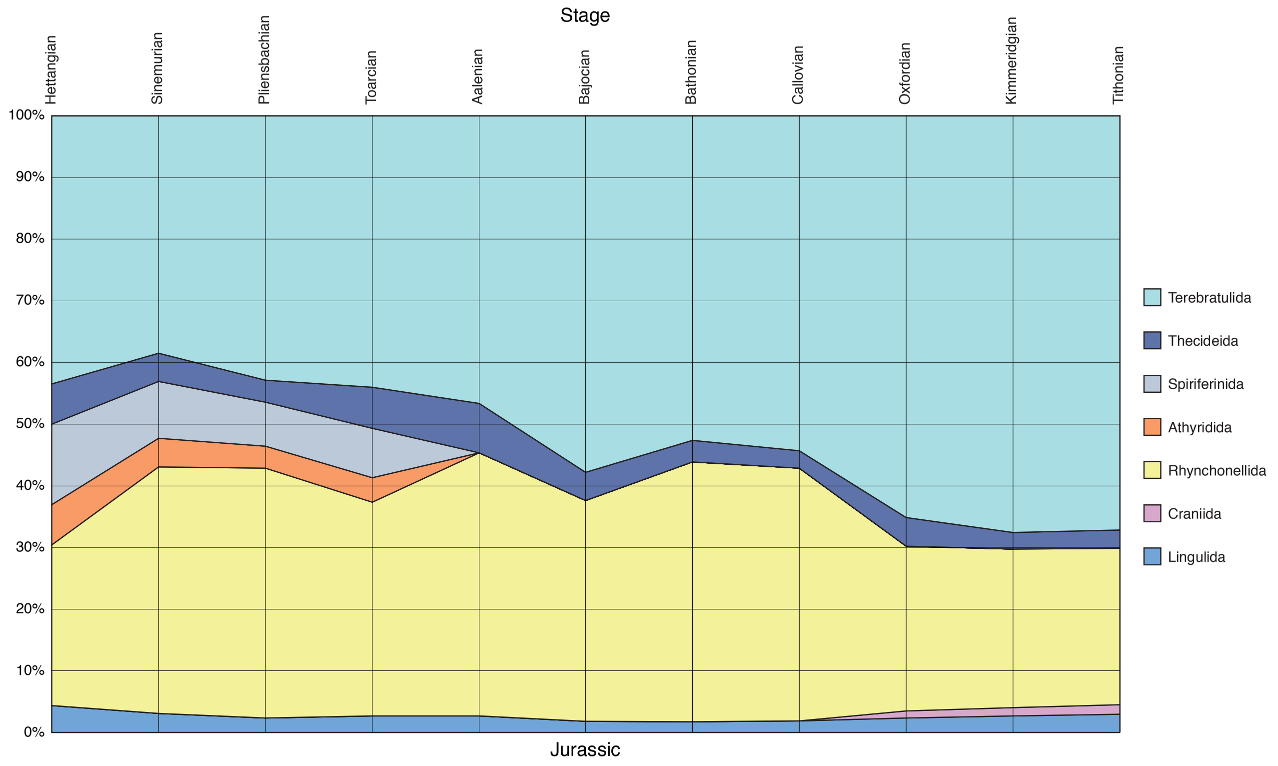

FIG. 1932. Relative proportions of different orders of brachiopods recorded from each of 11 stages of the Jurassic System, with lowermost stage (Hettangian) on left-hand side of horizontal axis, and uppermost Tithonian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present (new).

have influenced the disappearance of the Spiriferinida and the Athyridida (Alvarez, 2006) and the post-Aalenian Stage conditions that might have contributed to the radiation of the Terebratulida. From isotopic evidence it appears that global climates did fluctuate during the Jurassic but with a much less wide range than in other parts of the geologic record (see compilation in Gradstein, Ogg, & Smith, 2004). There were, however, several pronounced negative excursions in the carbon isotope record during the Jurassic (Jenkyns & others, 2002). The most dramatic of these and, indeed, one of the largest carbon isotope excursions recorded throughout the Phanerozoic (Hesselbo, Grocke, & Jenkyns, 2000), occurred during the early Toarcian Stage (McArthur & others, 2000). This event, which coincided with the deposition of extensive organic-rich sediments such as the Jet Rock in England, is believed to represent a major oceanic anoxic event, although this and many other similar events may also have represented the culmination in periods of enhanced oceanic productivity that increased the rate of organic carbon burial (see discussion in Cretaceous section below). Although lasting for only 0.5 million years and composed of several pulses (McArthur & others, 2000), this event seems to have had a dramatic impact on brachiopod diversity and probably contributed to the extinction of two orders (the Athyridida and Spiriferinida) that were long lived (from the Upper Ordovician [Costonian] and Lower Devonian), and which had been present, albeit in small numbers of genera, throughout the Lower Jurassic (Fig. 1932).

If the global spread of anoxic conditions or enhanced organic carbon deposition did indeed contribute to the extinction of the Athyridida and the Spiriferinida, then it may also have had a discernible effect on the Rhynchonellida, which declined from 34 genera in the Pliensbachian Stage to 26 genera in the Toarcian Stage, before their diversity increased to 32 genera in the Aalenian Stage and 39 in the Bathonian Stage. Simple diversity counts will not take into account evolutionary innovations among constituents of the lineages, but the raw abundance data suggests that Terebratulida were much less affected by events during the Toarcian Stage. Terebratulida generic abundances were 36 in the Pliensbachian Stage and 33 in the overlying Toarcian Stage, before increasing again to 35 genera in the lowermost Middle Jurassic Aalenian Stage and climbing to 63 genera in the overlying Bajocian Stage. By the Bathonian Stage a total of 60 genera of Terebratulida are recorded, as compared with 57 genera in the uppermost Middle Jurassic Callovian Stage. The implication is that Terebratulida were able to survive, or recover from, a global reduction in the oxygenation levels of the ocean better than any other brachiopod stock. The data also suggest that they were better equipped to exploit the post-Toarcian Stage recovery to more normal oxygen conditions; although Terebratulida recovery initially appears to be slower than that of the Rhynchonellida, in the long run it was more sustained.

Even though Terebratulida became by far the dominant component of brachiopod faunas in the Upper Jurassic, the absolute numbers of Terebratulida genera declined, however, from a high of 63 genera in the Middle Jurassic Bajocian Stage to a low of 45 genera in the uppermost Tithonian Stage of the Upper Jurassic. There was another major negative carbon oxygen excursion in the Upper Jurassic Oxfordian Stage (Padden, Weissert, & de Rafelis, 2001), again thought to indicate the spread of anoxic or low-oxygen conditions in the oceans following the release of methane into the atmosphere from gas hydrates. This event was marked by the deposition of sediments with high organic contents (e.g., black shales), due to the decay of enhanced quantities of organic material that brought about a reduction in oxygen levels. Along with a series of smaller events during the Jurassic, such environmental stresses may have influenced the diversity of Terebratulida subsequent to their peak in the Bathonian

Stage. There was, however, a major, positive excursion in carbon isotope ratios in the Bajocian Stage (see composite curve in GRADSTEIN, OGG, & SMITH, 2004), and brachiopods achieved their greatest Jurassic diversity in that stage and in the overlying Bathonian Stage. These two stages are also characterized by the highest ever diversity of Terebratulida in any one stage (with the exception of the Holocene, which is anomalous in containing extant genera). It may also be that the subsequent progressive decline in brachiopod diversity in the Upper Jurassic is due to other factors, such as changes in the sedimentary environments, especially if they were particularly pronounced in shallow marine areas from which the majority of brachiopods recorded in these stages have been described. The low overall number of brachiopods may also make them much more vulnerable to exposure issues. It has been estimated that the exposure of Jurassic rocks (in terms of km^2 per year) is much lower than for the preceding Permian and Triassic Systems (RAUP, 1976).

CRETACEOUS SYSTEM

In the Cretaceous System (145.5 ± 4.0 Ma to 65.5 ± 0.3 Ma; GRADSTEIN, OGG, & SMITH, 2004), brachiopod diversity remained fairly constant at around 70 to 85 genera during the Lower Cretaceous Berriasian to Albian Stages (Fig. 1933). The lowermost Cenomanian Stage of the Upper Cretaceous had a very similar number of genera (74), but brachiopod diversity declined noticeably in the Turonian Stage (to 58 genera), and similarly low diversities were maintained in the overlying Coniacian and Santonian Stages (56 and 59 genera respectively; Fig. 1933). The number of genera increased again in the Campanian (72 genera) and in the succeeding Maastrichtian Stage (75 genera), the uppermost stage of the Upper Cretaceous. The same five orders present at the end of the Jurassic persisted throughout the Cretaceous System, but their relative proportions varied (Fig. 1934). The Terebratulida are the dominant stock in all Cretaceous stages but range from a high of 81% of the total brachiopod fauna in the Lower Cretaceous Aptian Stage to a low of 58% in the Upper Cretaceous Campanian Stage. The overall trend, especially in the Upper Cretaceous, is for the proportion of the total fauna represented by the Terebratulida to decline (Fig. 1934). The Rhynchonellida represent only 10% of the total fauna during the Aptian stage, but contribute between 19% and 24% of the total fauna throughout all stages of the Upper Cretaceous. The Thecideida, and to a lesser extent, the Craniida, contribute an increasing proportion of the fauna in the uppermost Campanian (11% and 6% respectively) and Maastrichtian Stages (12% and 7% respectively) of the Cretaceous System.

The total number of brachiopod orders recorded during the Cretaceous drops to 5 out of the total of 26, the lowest of any system since the beginning of the Cambrian System. This low taxonomic diversity follows the disappearance of the Athyridida and the Spiriferinida in the Jurassic. Throughout the Cretaceous, representatives of the Terebratulida are dominant, and in the 6 stages of the Lower Cretaceous their generic diversity is very consistent, varying between 55 and 58 genera. Terebratulida diversity in the lowermost Upper Cretaceous Cenomanian Stage was at 52 genera but thereafter dropped to 38, 35, and 36 genera respectively in the Turonian, Santonian, and Coniacian Stages of the middle Upper Cretaceous. The uppermost two stages of the Upper Cretaceous witnessed a slight recovery in Terebratulida diversity, up to 42 genera in the Campanian Stage and 44 genera in the Maastrichtian Stage.

The Rhynchonellida are the second most abundant component of Cretaceous brachiopod faunas, reaching a maximum diversity of 19 genera in the middle Lower Cretaceous Hauterivian Stage and then declining to only 7 genera in the upper Lower Cretaceous Aptian Stage. Throughout their geologic history the Rhynchonellida do appear to be particularly prone to fluctuating diversity

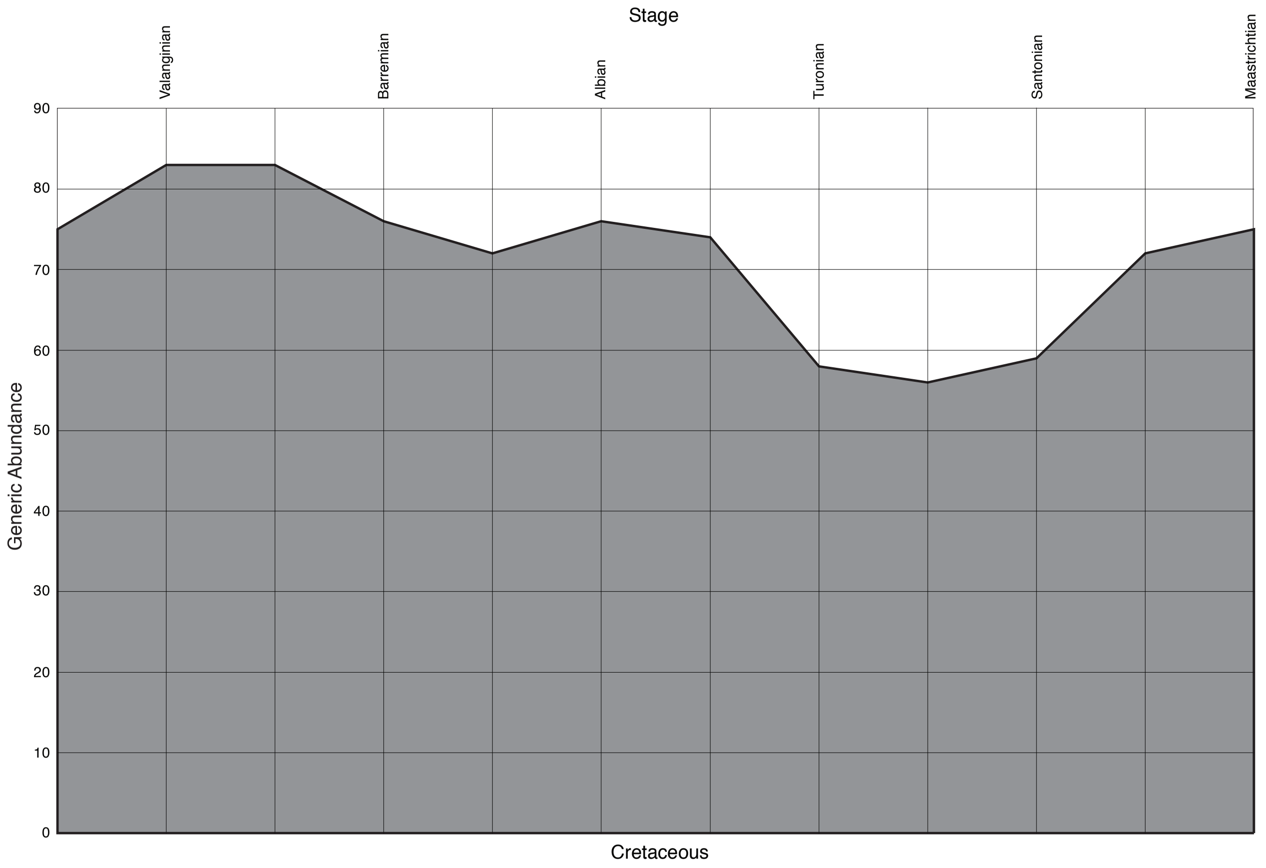

FIG. 1933. Abundance of brachiopods in each of 12 stages (horizontal axis) assigned to Cretaceous System, with lowermost stage (Berriasian) on left-hand side of horizontal axis and uppermost Maastrichtian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

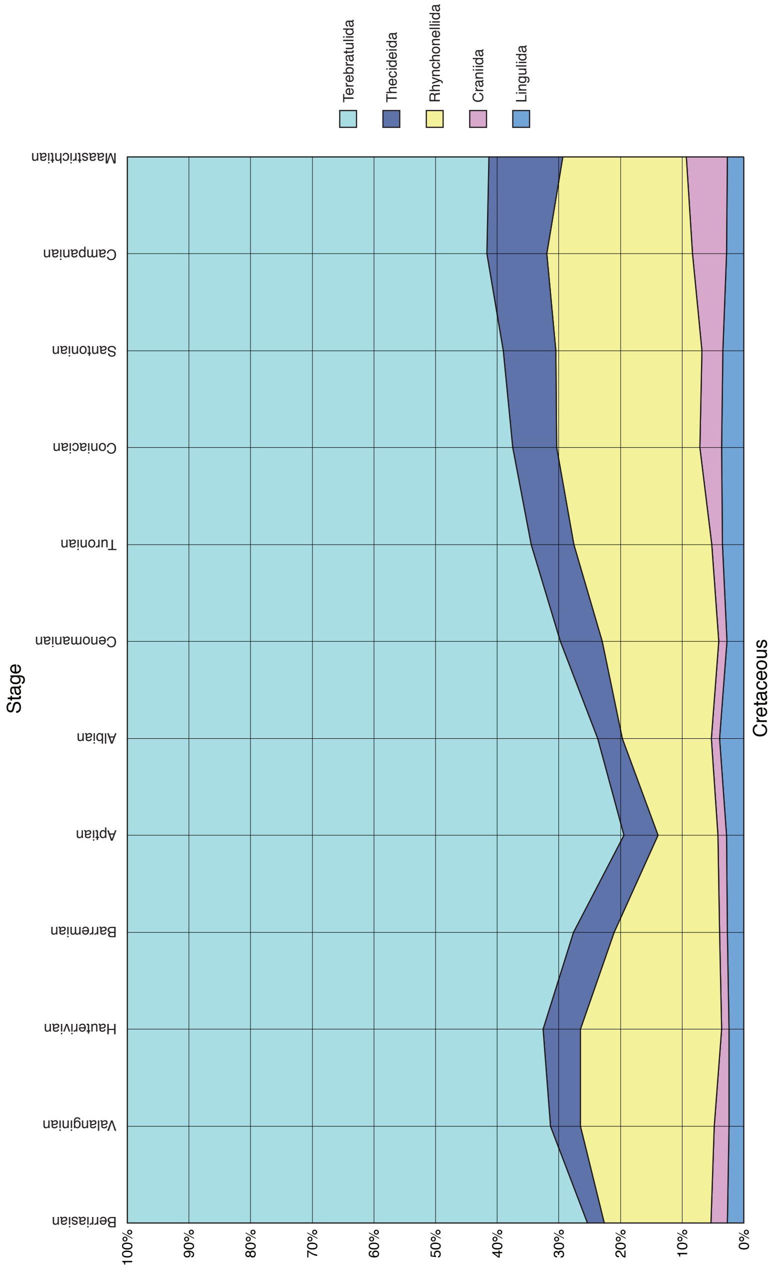

Fig. 1934. Relative proportions of different orders of brachiopods recorded from each of 12 stages of Cretaceous System, with lowermost stage (Berriasian) on left-hand side of horizontal axis and uppermost Maastrichtian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present (new).

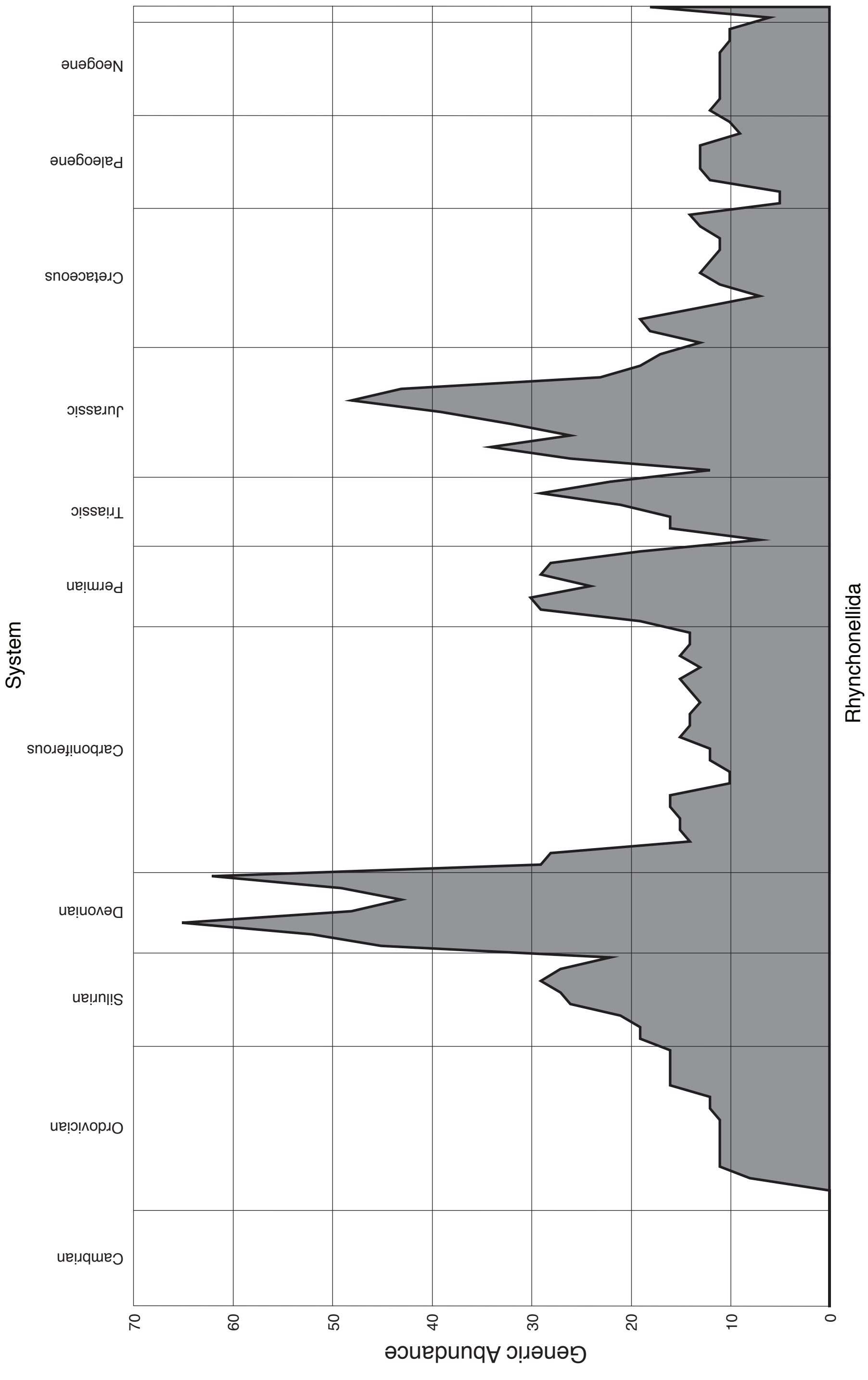

FIG. 1935. Stratigraphic distribution of order Rhynchonellida, demonstrating great longevity and considerable fluctuations in diversity. Three systems display 2 well-defined peaks of Rhynchonellida diversity (Devonian, Permian, and Jurassic). Far right, unlabelled segment of diagram portrays Rhynchonellida distribution in Pleistocene and Holocene stages (new).

(Fig. 1935), although to some extent this may be due to artefacts associated with the taxonomic procedures applied to Rhynchonellida (such as the practice of treating Paleozoic and Mesozoic genera separately). Rhynchonellida generic numbers recovered to 11 in the uppermost Lower Cretaceous Albian Stage and remain comparatively high, at 13 to 17 genera, throughout all stages of the Upper Cretaceous. The Thecideida reached a maximum diversity in the Late Cretaceous of 9 genera; for the earlier part of the system there are only 3 to 5 genera present. For most of the Cretaceous the only surviving linguliforms are the Lingulida and Craniida, and these two orders are represented by a combined total of only 3 or 4 genera; in the Upper Cretaceous Campanian and Maastrichtian Stages, however, the number of Craniida genera increases to 4 and 5 respectively.

Overall, the Cretaceous witnessed relatively low numbers of brachiopod genera. During the Jurassic the total numbers of genera peaked at 114 (in the Bathonian Stage), but the maximum number of genera recorded in any Cretaceous stage was 83 genera (in the Valanginian and Hauterivian Stages) and the mean number of genera in the six stages of the Upper Cretaceous was 66.

The most distinctive feature of brachiopod stratigraphic distribution in the Cretaceous is the decline in absolute numbers of genera in the Turonian stage, a decline that persisted into the overlying Coniacian and Santonian Stages. Brachiopod diversity again seems to have been adversely affected by global events at the Cenomanian-Turonian boundary, the physical evidence of which is a significant horizon of organic-rich sediments that has been recorded globally. This event, known as the Oceanic Anoxic Event 2, or the Bonarelli Event, is also marked by a pronounced carbon isotope excursion (Jenkyns, Gale, & Corfield, 1994). While establishing direct links between such events and brachiopod diversity seems likely, such suggestions must be treated with caution given the provisos mentioned at the beginning of this chapter. It is plausible, however, to envisage a situation in which the widespread accumulation of organic-rich sediments created problems for brachiopods that had previously colonized areas of quite different sedimentation. The evidence from the global survey of brachiopod diversity presented in the *Treatise* seems to imply that low-oxygen conditions may have had a profound effect on the phylum and at least contributed to a 22% reduction of the number of brachiopod genera between the Cenomanian and Turonian Stages.

PALEOGENE, NEOGENE, PLEISTOCENE, AND HOLOCENE

Although representing the last 65.5 million years of geologic history, the 18 stages from the beginning of the Paleogene (65.5 ± 0.3 Ma to 23.04 ± 0 Ma; Gradstein, Ogg, & Smith, 2004) to the present day will be discussed together, as brachiopod diversities were low throughout, and the phylum represents minor constituents of marine faunas. That is not to imply that the stratigraphic distribution of brachiopods over the last 65.5 million years is without interest. The lowermost Danian Stage of the Paleogene includes a total brachiopod fauna of 35 genera, the third lowest in their geologic record (Fig. 1936) and one of the largest percentage declines in their history, in which there was a 53% reduction in the number of the brachiopod genera compared to the preceding uppermost Cretaceous Maastrichtian Stage. The succeeding Thanetian Stage witnessed a further reduction, down to a total of 26 genera, the second lowest diversity of any stage in the Phanerozoic and again one of the most significant percentage declines in their geologic history (representing a reduction of 26% in the total number of brachiopod genera compared to the Danian Stage). Over a period of 11.4 million years from the end of the Cretaceous, therefore (i.e., the duration

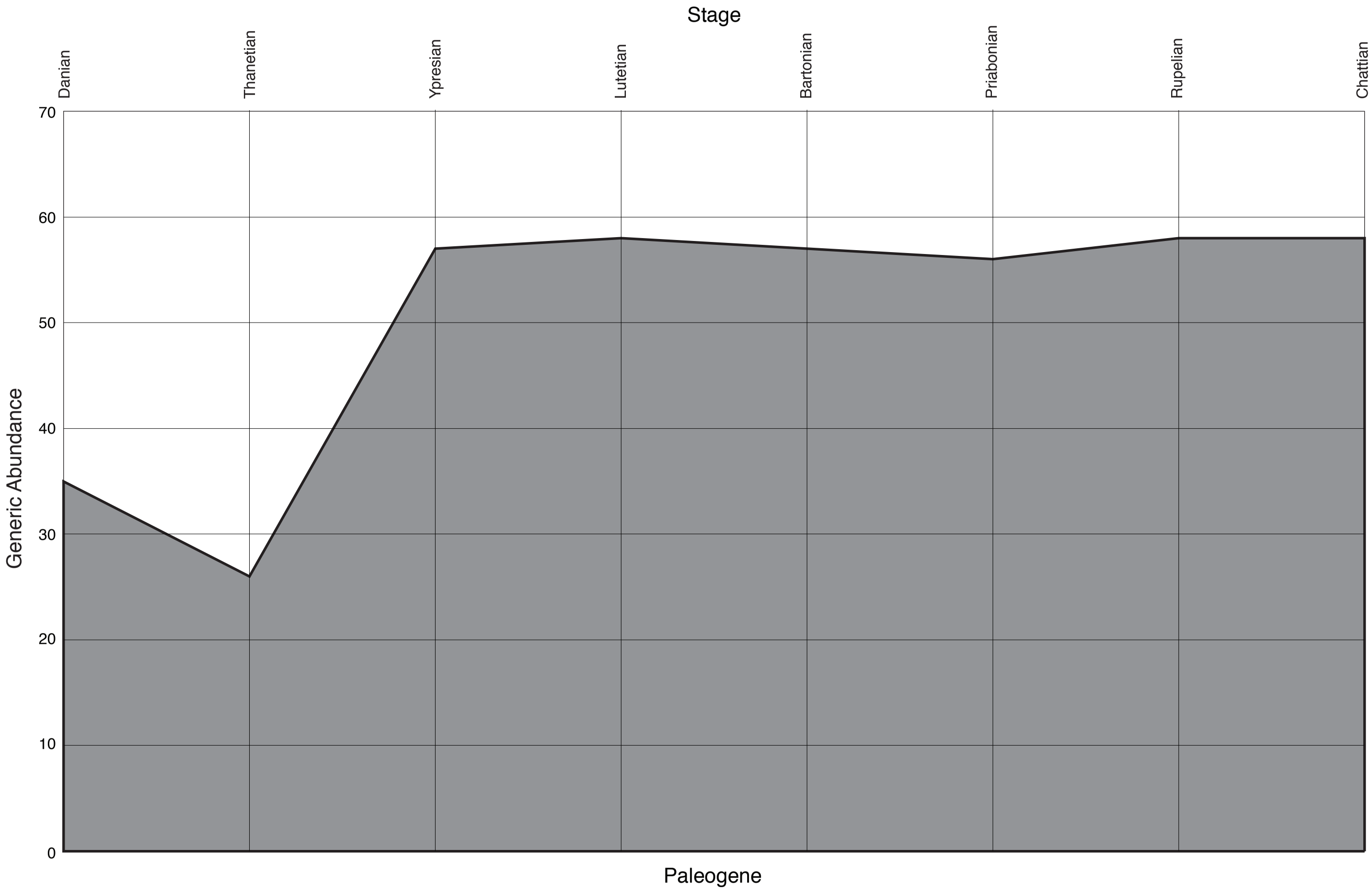

FIG. 1936. Abundance of brachiopods in each of 8 stages (horizontal axis) assigned to Paleogene System, with lowermost stage (Danian) on left-hand side of horizontal axis and uppermost Chattian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

of the Danian and Thanetian Stages, which together comprise the Paleocene Series), brachiopod diversities declined dramatically. In GRADSTEIN, OGG, and SMITH (2004) the duration of the Paleocene has been reduced to a still significant 10.3 million years (and a new stage, the Selandian, has been established between the Danian and Thanetian Stages).

The event that precipitated such a long-lived decline in brachiopod diversities was of course the end-Cretaceous extinction, by far the most studied event of its type (MACLEOD & KELLER, 1996). For some years extensive evidence has been presented that seemed to indicate that the extinction event was primarily related to the impact of an extraterrestrial body, in particular an asteroid that left a crater at Chicxulub, off the Yucatan Peninsula (ALVAREZ & others, 1980). This assertion has recently been challenged, however, by the suggestion that the Chicxulub impact crater actually occurred around 300,000 years before the Cretaceous-Paleogene boundary (KELLER & others, 2003; KELLER, ADATTE, & STINNESBECK, 2003). An alternative, or complementary, explanation is that the end-Cretaceous extinction event was caused by severe environmental change brought about by much greater than normal levels of volcanic activity at the time (i.e., the formation of the Deccan Traps in Asia and the volcanism associated with the opening of the Atlantic Ocean). In this scenario (MCLEAN, 1985), the Earth's atmosphere, climate, and oceans were subjected to major perturbation (e.g., sulphur dioxide aerosols from volcanic eruptions in the stratosphere inducing cooling and enhanced concentrations of toxic trace elements).

Isotopic evidence from marine microorganisms suggests that ocean temperatures during the Mid-Cretaceous were very high (more than 10 °C higher than today; HUBER, NORRIS, & MACLEOD, 2002) but had declined progressively from a maximum in the Turonian. Some groups of organisms appear to have been unaffected by the end-Cretaceous event (MACLEOD & others, 1997), however, including representatives of phyla that would be expected to be particularly vulnerable to such radical environmental disturbances. Certainly some brachiopod workers have drawn attention to the fact that the phylum was relatively unaffected by this extinction event (AGER, 1988). It may well be, therefore, that the notoriety of the end-Cretaceous extinction may well have increased the proportion of pseudoextinctions (as taxonomists expect to find different taxa on either side of the stratigraphic boundary). Certainly taxonomic procedures are thought to have a significant effect on ancient biodiversity studies (SHEEHAN, 1977).

Whatever the cause, or causes, of the extinction, just over half the brachiopod genera recorded in the uppermost Maastrichtian Stage of the Cretaceous became extinct by the lowermost Danian Stage of the Paleogene (Fig. 1936). In percentage terms this sustained decline is exceeded in brachiopod history only by that recorded at the Permian-Triassic boundary. The much lower number of brachiopod genera in the Late Cretaceous and Paleocene suggests that any conclusions must be treated with great caution, however, as artefacts of preservation, exposure, and taxonomic practice will be proportionately much more significant at this extinction event.

Post-Thanetian Stage, the number of brachiopod genera recovered to a total of between 56 and 58 genera throughout the 6 stages that make up the Eocene and the Oligocene Series of the Paleogene System. Brachiopod generic numbers increased again during the 6 stages of the Miocene Series (the lower part of the Neogene System; 23.04 ± 0 Ma to 1.81 ± 0 Ma; GRADSTEIN, OGG, & SMITH, 2004) at a very consistent level of 72 to 74 genera. In the two stages of the Pliocene Series (the upper part of the Neogene System) brachiopod generic abundances remained very similar at 68 genera in both the Zanclean and the Piacenzian Stages (Fig. 1937). The apparent slight decline in brachiopod diversity in the

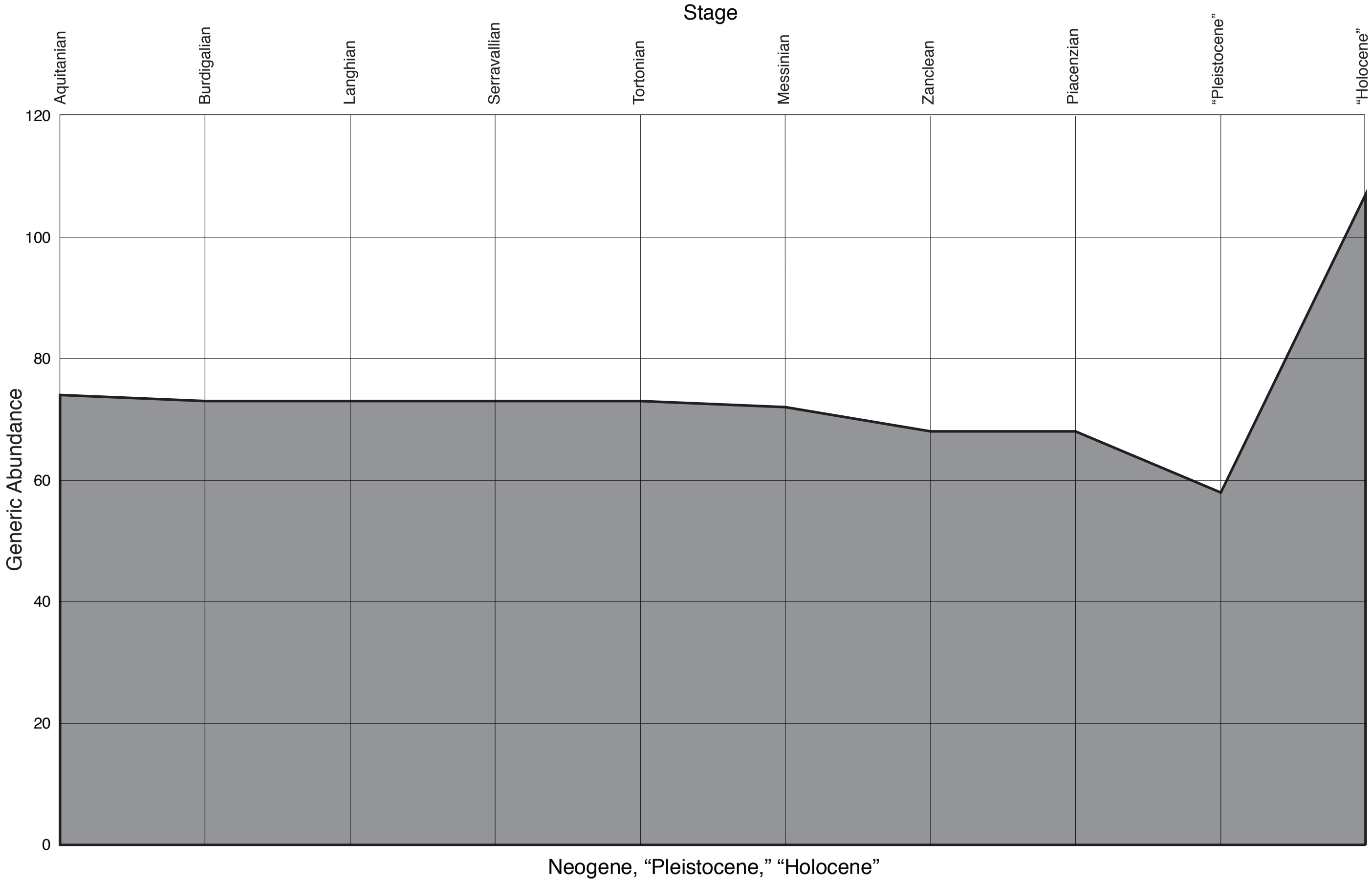

FIG. 1937. Abundance of brachiopods in each of 8 stages (horizontal axis) assigned to Neogene System (from lowermost Aquitanian Stage on left-hand side of diagram to uppermost Piacenzian Stage), along with Pleistocene and Holocene stages (latter including Recent genera). Stage nomenclature, common abbreviations, meaning of quotation marks, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

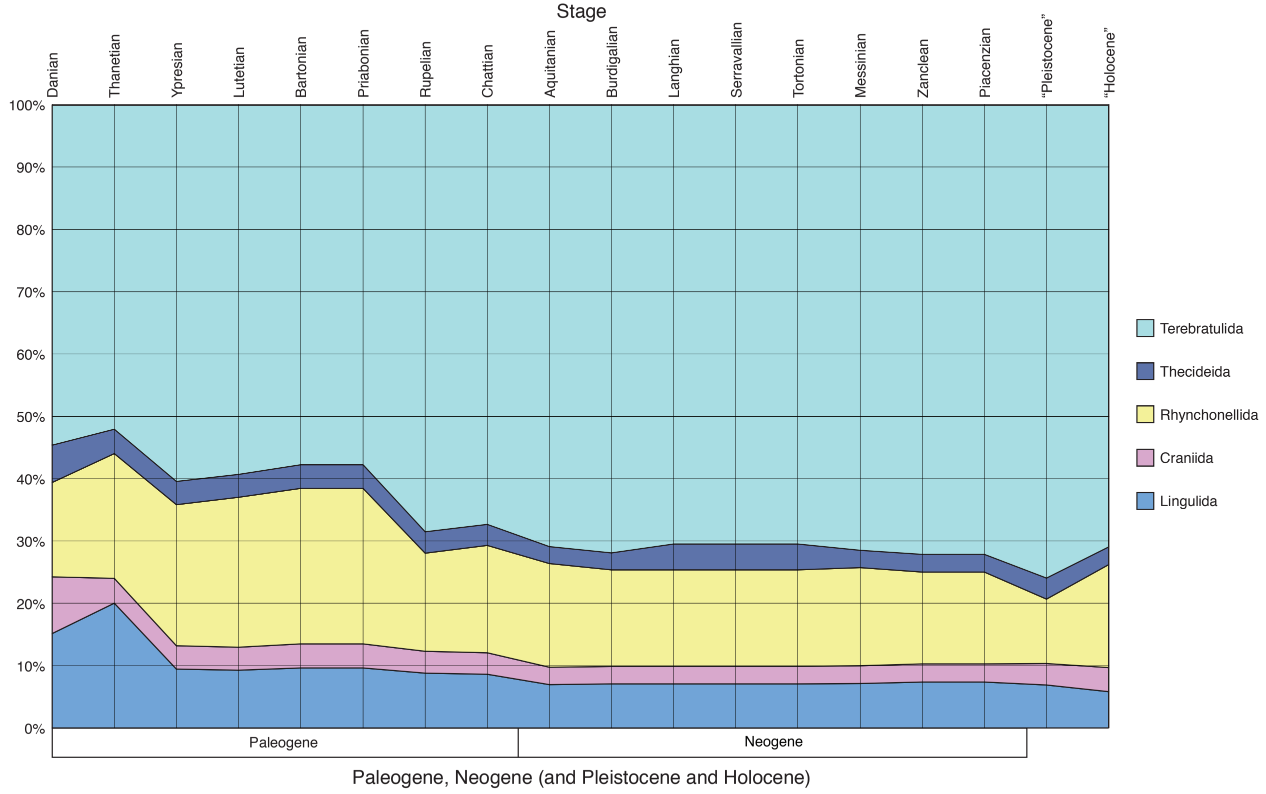

FIG. 1938. Relative proportions of different orders of brachiopods recorded from each of 8 stages of Paleogene System (Danian to Chattian), 8 stages of overlying Neogene System (Aquitanian to Piacenzian), and Pleistocene and Holocene stages (latter including Recent genera). Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present; see Table 40 for meaning of quotation marks (new).

Pleistocene (to below 60 genera; 1.81 ± 0 Ma to 0.01 ± 0 Ma; Gradstein, Ogg, & Smith, 2004) and the subsequent dramatic increase to 107 genera in the Holocene (including Recent genera; 0.01 ± 0 Ma to present day; Gradstein, Ogg, & Smith, 2004) are almost certainly artefacts of the fossil record. Many Pleistocene deposits are unconsolidated (hence prone to erosion and poor exposure), and marine successions of this stage are often inaccessible (in sediment accumulations on the seabed). The 84% increase in brachiopod genera recorded in the present day perhaps provides a crude estimate of the incompleteness of the fossil record, because there are no indications of major evolutionary innovation among extant stocks and the expansion is most likely due to the better preservation and information content of Recent, as compared to fossil, specimens.

Little has changed taxonomically over the last 65 million years (Fig. 1938). The same five orders that were present during the Cretaceous occur throughout these intervals of Earth history. The dominance of the Terebratulida continued and indeed increased through this period of Earth history, to such an extent that over 70% of brachiopod genera were Terebratulida in all stages from the base of the Neogene System. In Recent seas, not only is the generic diversity of Terebratulida comparatively high (75 genera representing 70% of the total fauna), but they also tend to occur in relatively high numbers. The diversity of Terebratulida rose consistently from about 20 genera at the start of the Paleogene System (i.e., the Danian Stage of the Paleocene Series) to 39 by the end of the system (i.e., in the two stages [Rupelian and Chattian] that make up the Oligocene Series). In all 6 stages assigned to the Miocene, Terebratulida diversities are very consistent at 52 or 53 genera. Such consistency is probably again influenced by the large numbers of Holocene Terebratulida genera that have been described due to their better accessibility. A total of 75 Holocene Terebratulida genera have been described, the highest number of representatives of this order recorded in any stage throughout their geologic history. Many of these genera have extensive geologic records that will range through stages in which brachiopods are poorly known due to exposure gaps. By comparison, the 1965 *Treatise* (Moore, 1965) recorded about 45 Holocene terebratulide genera. The Rhynchonellida, continuing to display the fluctuations in diversity that are evident throughout their geologic history, increased from about 5 genera at the start of the Paleocene to 13 in three stages in the middle of the system, reduced slightly in numbers to range from 10 to 12 throughout the 8 stages that make up the Neogene System (i.e., the Miocene and Pliocene), and then increased to 18 genera at the present day (i.e., the Holocene stage).

During these intervals of Earth history the number of Lingulida genera increased to 5, while Craniida diversity mostly remained at 2 genera, although it has increased to 4 genera in recent times. Representatives of the other extant order, the Thecideida, declined somewhat to between 2 and 3 genera over this time span, but 3 genera from this order are still living today.

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