The Fossil Record 2

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PREFACE

The present volume had its origin in 1987, when Michael Whyte and the editor approached the Palaeontological Association with the idea of an update of *The Fossil Record* published by the Geological Society of London in 1967. That volume had resulted from discussions between the Geological Society of London and the Palaeontological Association, and followed a meeting held in 1965. The most valuable part of the original publication had been the extensive documentation of families, and we decided to focus on that aspect, and not to include any analytical or commentary papers in the present volume, or to hold a meeting.

The 1967 *Fossil Record* was produced by nine editors and 125 contributors, and amounted to 827 pages. The 1993 edition was produced by one editor and 90 contributors, and amounts to 845 pages: a sure sign of increasing efficiency by the palaeontological community! Of the original 125 contributors, only eight have been involved in the present edition (P. Copper, W. T. Dean, B. G. Gardiner, L. B. Halstead (= L. B. H. Tarlo), M. R. House, C. Patterson, R. B. Rickards and A. W. A. Rushton). Of the 1967 contributors, 105 are listed with UK addresses, nine from the United States of America, four from Australia, three from France, two from the Republic of Ireland, and one each from Canada and The Netherlands (i.e. 84% of the authors were British). Comparative figures for the present edition are that 61 of the 90 contributors are based in the UK, 12 in the United States, four in each of France and the Republic of Ireland, two in each of Australia and Canada, and one in each of China, Germany, Jamaica, the former USSR and Sweden. The British contingent represents 68% of the total of authors. The rise in non-British authors from 16% in 1967 to 32% in 1992 could be interpreted as a laudable move to internationalize the project: equally, the fall from 84% to 68% could indicate the relative decline of palaeontology in Britain over the past 25 years (indeed, many of the British contributors to the present edition, 18 of the 61) are graduate students, postdoctoral scientists or essentially unemployed.

RATIONALE

To many palaeobiologists, of course, this kind of enterprise is highly suspect. The reasons for this view are not hard to find. For example, it will be possible for experts to criticize nearly every entry since the authors have had to make difficult decisions concerning which taxa to include in a family and which to exclude, how to deal with questionable and incomplete material, how to treat specimens of uncertain age, and how to divide up the families. However, the scope of this publication has allowed authors to comment on all of these kinds of complex issues. Hence, users of the data will be able to decide how to code the information, whether to include families represented by single species or not, how to deal with incomplete and poorly defined early records, how to interpret uncertain stratigraphical assignments and so on.

One of these problems may be insurmountable for many critics: the validity of families, or indeed of any other higher taxon. How are families to be determined and how are they to be rendered comparable between bacteria and mammals, or between trilobites and birds? There is no counter-argument other than practicality. Our view has been that, if it is worth studying large-scale evolutionary patterns, palaeobiogeographical distributions, and other macro-evolutionary phenomena, one has to have some raw data to work with. Better to have a 1993 database, shot through with errors as it may be, than to continue to use a 1967 listing *faute de mieux*. The critics might have been partially disarmed by a generic-level listing, or even a species-level listing, but these would have entailed other kinds of scientific problems, as well as the practical ones of finding authors with the stamina to complete the task, and a publisher with the generosity to deal with such a monster.

There have also been criticisms that the stratigraphical stage (or epoch for the Precambrian, Cambrian, Ordovician, Silurian, Carboniferous, Miocene and Pleistocene) is too crude and can be improved upon for many groups. While this is doubtless true for certain marine fossils used in biostratigraphy, it would have been impossible to go to substages or zones for most groups. Indeed, it was hard enough to achieve stage-level accuracy for many terrestrial groups! Hence, the family and the stage (or epoch, as noted) were chosen as the most appropriate working units for this volume. None the less, where possible, many authors have used stage-level terminology for the Palaeozoic and Cainozoic erathems.

DATA COMPILATION

The editor decided to follow broadly the chapter divisions used in *The Fossil Record* (1967), and to commission authors/editors who would oversee each major group. Each of these was to use their specialist knowledge of the phylum – or other major group – in question, to select and commission portions of the text, and then to compile the whole chapter, plugging gaps and providing an overview. The first letters inviting contributions went out in mid-1988, and several chapters were successfully allocated in this way.

As time went on, it became clear that it would not be possible to complete the book in such a simple fashion: in many cases, appropriate authors did not exist, or they had other commitments that prevented them from completing the work on time. Early in 1990, Chapman & Hall agreed to publish the book and, later that year, generous grants were received from the Linnean Society (administering the NERC Taxonomic Publications Grant), the Royal Society (a Scientific Publications Grant), and the Palaeontological Association. This money was used to pay for the completion of certain chapters and parts of chapters (1, 3–6, 8, 10, 11, 13–16, 18–21, 28, 29, 42, 45) that otherwise could not

Eono-them	Era-them	Sub-erathem, System, Sub-system	Series	Stage	Alternative stage Designations
Phanerozoic	Cainozoic	Quaternary Q	Holocene	HOL	
			Pleistocene	PLE	
		Tertiary / Neogene Ng	Pliocene PLI	Piacenzian PIA	
				Zanclian ZAN	
			Miocene UMI	Messinian MES	
				Tortonian TOR	
			MMI	Serravallian SRV	
				Langhian LAN	
			LMI	Burdigalian BUR	
				Aquitanian AQT	
		Tertiary / Palaeogene Pg	Oligocene OLI	Chattian CHT	
				Rupelian RUP	
			Eocene EOC	Priabonian PRB	
				Bartonian BRT	
				Lutetian LUT	
				Ypresian YPR	
			Palaeocene PAL	Thanetian THA	
				Danian DAN	
	Mesozoic	Cretaceous K	Senonian SEN	Maastrichtian MAA	
				Campanian CMP	
				Santonian SAN	
				Coniacian CON	
			Gallic GAL	Turonian TUR	
				Cenomanian CEN	
				Albian ALB	
				Aptian APT	
				Barremian BRM	
			Neocomian NEO	Hauterivian HAU	
				Valanginian VAL	
				Berriasian BER	Ryazanian RYA
		Jurassic J	Malm MLM	Tithonian TTH	Portlandian POR
				Kimmeridgian KIM	
				Oxfordian OXF	
			Dogger DOG	Callovian CAL	
				Bathonian BTH	
				Bajocian BAJ	
				Aalenian AAL	
			Lias LIA	Toarcian TOA	
				Pliensbachian PLB	
				Sinemurian SIN	
				Hettangian HET	
		Triassic Tr	Upper u	Rhaetian RHT	
				Norian NOR	
				Carnian CRN	
			Middle m	Ladinian LAD	
				Anisian ANS	
			Scythian SCY	Spathian SPA	Smithian SMI / Olenekian OLK
				Nammalian NML	Dienerian DIE / Induan IND
				Griesbachian GRI	
	Palaeozoic	Permian P	Zechstein ZEC	Changxingian CHX	Ochoan OCH / Tatarian TAT / Dorashamian DOR
				Longtanian LGT	Djulfian/Dzhulfian DZH
				Capitanian CAP	Guadalupian GUA / Kazanian KAZ
				Wordian WOR	
				Ufimian UFI	
			Rotliegendes ROT	Kungurian KUN	Roadian ROD / Leonardian LEN
				Artinskian ART	
				Sakmarian SAK	Wolfcampian WOL
				Asselian ASS	

Fig. P.1 The geological time scale used in *The Fossil Record 2*, Permian to Recent.

Eono-them	Era-them	Sub-erathem, System, Sub-system		Series		Stage		Alternative stage Designations		
Phanerozoic	Palaeozoic	Carboniferous C	Pennsylvanian C(u)	Gzelian	GZE	Noginskyian	NOG	C	Stephanian STE	Silesian SLS
						Klazminskyian	KLA	B		
				Kasimovian	KAS	Dorogomilovskian	DOR	A		
						Chamovnicheskian	CHV			
						Krevyakinskian	KRE	Cantabrian CTB		
				Moscovian	MOS	Myachkovskian	MYA	D	Westphalian WPH	
						Podolskian	POD	C		
						Kashirskian	KSK	B		
						Vereiskian	VRK			
				Bashkirian	BSK	Melekesskian	MEL	A		
						Cheremshanskian	CHE			
						Yeadonian	YEA	C	Namurian NAM	
						Marsdenian	MRD	B		
						Kinderscoutian	KIN			
			Mississippian C(l)	Serpukhovian	SPK	Alportian	ALP	A		
						Chokierian	CHO			
						Arnsbergian	ARN			
						Pendleian	PND			
				Visean	VIS	Brigantian	BRI	Dinantian DIN		
						Asbian	ASB			
						Holkerian	HLK			
						Arundian	ARU			
						Chadian	CHD			
				Tournaisian	TOU	Ivorian	IVO			
						Hastarian	HAS			
		Devonian D		Upper	u	Famennian	FAM			
						Frasnian	FRS			
				Middle	m	Givetian	GIV			
						Eifelian	EIF			
				Lower	l	Emsian	EMS			
						Pragian	PRA	Siegenian SIG		
						Lochkovian	LOK	Gedinnian GED		
		Silurian S		Pridoli	PRD					
				Ludlow	LUD	Ludfordian	LDF			
						Gorstian	GOR			
				Wenlock	WEN	Homerian	HOM	Gleedonian GLE		
								Whitwellian WHI		
						Sheinwoodian	SHE			
				Llandovery	LLY	Telychian	TEL	Fronian FRO		
						Aeronian	AER	Idwian IDW		
						Rhuddanian	RHU			
		Ordovician O	Bala BAL	Ashgill	ASH	Hirnantian	HIR			
						Rawtheyan	RAW			
						Cautleyan	CAU			
						Pusgillian	PUS			
				Caradoc	CRD	Onnian	ONN			
						Actonian	ACT			
						Marshbrookian	MRB			
						Longvillian	LON			
						Soudleyan	SOU			
						Harnagian	HAR			
						Costonian	COS			
			Dyfed DFD	Llandeilo	LLO	Late	LLO3			
						Middle	LLO2			
						Early	LLO1			
				Llanvirn	LLN	Late	LLN2			
						Early	LLN1			
			Canadian CND	Arenig	ARG					
				Tremadoc	TRE					

Fig. P.1 The geological time scale used in *The Fossil Record 2*, Ordovician to Carboniferous.

Eono-them	Era-them	Sub-erathem, System, Sub-system	Series	Stage	Alternative stage Designations
Phanerozoic	Palaeozoic	Cambrian	Merioneth MER	Dolgellian DOL	
				Maentwrogian MNT	
			St David's STD	Menevian MEN	
				Solvan SOL	
			Caerfai/ Comley CRF	Lenian LEN	Toyonian TOY
				Atdabanian ATB	Botomian BOT
		€		Tommotian TOM	
Precambrian	Proterozoic	Sinian	Ediacara EDI	Poundian POU	
				Wonokan WON	
		Vendian	Varanger VAR	Mortensnes MOR	
		V		Smalfjord SMA	
		Sturtian		STU	
		Riphean		Karatau KAR	
				Yurmatin YUR	
			RIF	Burzyan BUZ	
		Animikean		ANI	
		Huronian		HUR	
	Archaen	Randian		RAN	
		Swazian		SWZ	
		Isuan		ISU	
		Hadean		HDE	
PЄ					

Fig. P.1 The geological time scale used in *The Fossil Record 2*, Archaean to Cambrian.

have been produced in time, and to assist with editorial costs.

Chapman & Hall paid for the production of the stratigraphical range charts, which were generated during 1991 and early 1992 from authors' texts by Ms Rachael Walker in Bristol, using the graphics software Canvas 2.1 on a Macintosh personal computer. The diagrams are on disc, and may be updated readily, or adapted for various uses.

STRATIGRAPHICAL FRAMEWORK AND OTHER STANDARDS USED

Authors were invited to use any stratigraphical scheme that they thought was appropriate, but to use those summarized in Harland *et al.* (1990) if they could. This was an attempt to standardize the stratigraphical periods and stages used, as well as the abbreviations, and of course involved no consideration of the exact ages in millions of years given by those authors. The relevant features of the stratigraphical scheme of Harland *et al.* (1990) are summarized in Fig. P.1, and some equivalent divisions of time used by some authors are also given. In addition, authors who used different schemes from the Harland *et al.* (1990) standard, have commented on this in their chapter introductions.

Other standards used in recording data are broadly as they were in the 1967 *Fossil Record* (see pp. 158–9 therein). The **First** and **Last** records of each family are given, based on published and unpublished data. Living families are indicated as **Extant**, although families with no fossil record are not always listed. For some groups, **Intervening** records are indicated, at stage level, to allow assessment of the gappiness (proportion of stages lacking fossils to stages with fossils) of the ranges quoted. Indeed, the measure of gappiness of intervening values can help to assess the likelihood of accuracy of the first and last records on a range bar, since error bars may be calculated (Strauss and Sadler, 1989).

An attempt was made to minimize the number of bibliographic references listed for each chapter, by referring to recent monographs and volumes of the *Treatise on Invertebrate Paleontology*, where available, for range records. Fuller documentation is presented where no such overview publications exist. Authors and dates of establishment of all taxa are also noted fairly completely, another great advance over the 1967 edition, but bibliographic data are **not** given for such authorships.

In the diagrams, all families, or family-equivalent taxa, are represented as noted by the author(s) of the chapters. Certain ranges are indicated by a solid line, and uncertain range terminations by a dashed line. No attempt is made in the charts to indicate gaps in the intervening range. Taxa with no fossil representatives are not shown on the charts.

In view of the shifting geography of eastern Europe and the former Soviet Union, the following terms are used throughout: 'former USSR', 'former Yugoslavia' and 'Germany'. Former Soviet regions revert to their former titles, e.g. 'Buryat SSR' becomes 'Buryatia'.

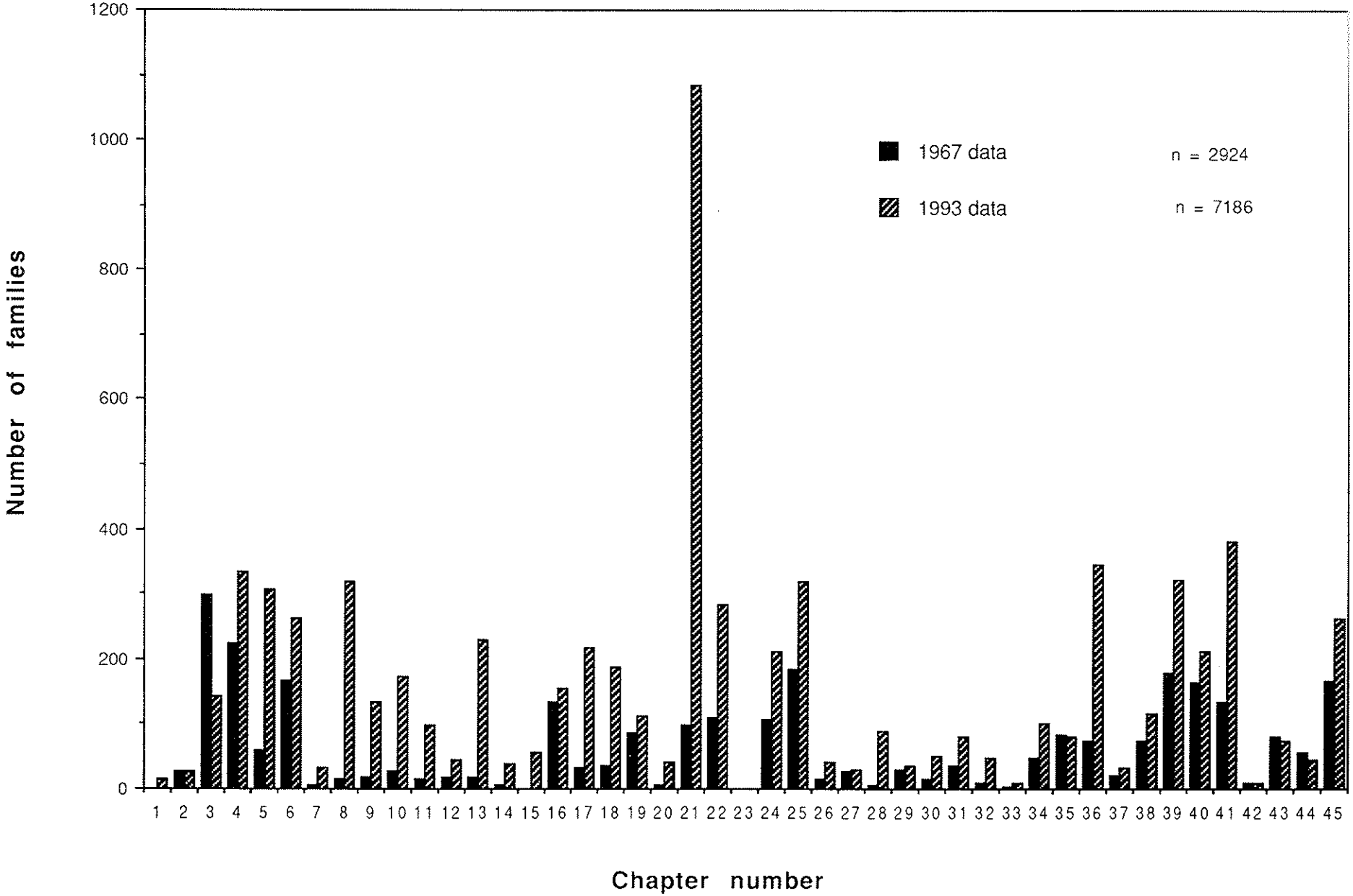

Fig. P.2 The number of families per chapter of *The Fossil Record 2*, compared to numbers in *The Fossil Record* (1967). Chapter 21 is Insecta.

Group	Number of families	
	1967	1993
1. Monera	0	14*
2. Fungi	28**	26
3. 'Algae'	298*	144
4. Protozoa	222	334
5. Porifera	59**	306
6. Coelenterata	168*	262
7. Mollusca: Amphineura, Monoplacophora	5**	32
8. Mollusca: Gastropoda	16**	318
9. Mollusca: Cephalopoda (Nautiloidea)	17**	133
10. Mollusca: Cephalopoda (pre-Jurassic Ammonoidea)	27**	174
11. Mollusca: Cephalopoda (post-Triassic Ammonoidea)	16**	97
12. Mollusca: Cephalopoda (Coleoidea)	18**	45
13. Mollusca: Rostroconchia, Scaphopoda, Bivalvia	18**	228
14. ?Mollusca incertae sedis	7**	40
15. Annelida	0	57
16. Arthropoda (Trilobita)	133*	154
17. Arthropoda (Aglaspidida, Chelicerata, Pycnogonida)	32**	217
18. Arthropoda (Crustacea, excluding Ostracoda)	36**	189
19. Arthropoda (Crustacea: Ostracoda)	86	113
20. Arthropoda (Euthycarcinoidea, Myriapoda)	6**	41
21. Arthropoda (Hexapoda: Insecta)	98**	1083
22. Brachiopoda	109*	282
23. Phoronida	0	1
24. Bryozoa	107*	212
25. Echinodermata	185*	319
26. Basal deuterostomes	14**	43
27. Graptolithina	28*	31
28. Problematica	6*	90
29. Miscellania	31*	35
30. Conodonta	16	52
31. Agnatha	36**	81
32. Placodermi	10**	49
33. Acanthodii	4**	9
34. Chondrichthyes	47*	100
35. Osteichthyes: basal actinopterygians	82	79
36. Osteichthyes: Teleostei	75**	345
37. Osteichthyes: Sarcopterygii	20	33
38. Amphibian-grade Tetrapoda	74*	115
39. Reptilia	178*	323
40. Aves	163	211
41. Mammalia	135**	381
42. Bryophyta	8*	9
43. Pteridophyta	81*	74
44. Gymnospermophyta	58*	44
45. Magnoliophyta ('Angiospermae')	167	261
TOTALS	2924	7186

Fig. P.3 Numbers of families recorded in the 1967 and 1993 editions of *The Fossil Record*. Key: *some taxa not divided to family level; **most taxa not divided to family level.

CHANGES SINCE 1967

Since 1967, a number of factors have combined to enhance the value of an updated second edition. Firstly, many more palaeobiologists than in 1967 are involved in research that requires accurate documentation of the fossil record, especially in the study of patterns of diversification, mass extinction, rates of evolution, clade shapes, completeness measures and phylogenetic bases of the data. Secondly, of course, much work has been done that will tend to change the nature of the family entries: systematic revisions of major groups, reassessments of numerous 'first' and 'last' taxa, discoveries of new fossils and revisions of stratigraphical schemes. All of these have resulted in a remarkable change in the database within 25 years: for example, Maxwell and Benton (1990) found that 416 out of 718 families of tetrapods (58%) listed in *The Fossil Record* (1967) had changed their durations in a 1987 compilation of data, and indeed most of these 416 changed families (57%) showed increased durations. Comparison of the independently compiled lists of marine animal families produced by Sepkoski (1982, 1992) shows similar large-scale changes in the database, here in the course of only ten years. It will be interesting to compare the 1967 and 1992 databases in similar ways in order to discover how much, and why, they have changed.

The Figs P.2 and P.3 indicate the numbers of families, or family-level equivalents identified for each major group in the 1967 and the 1992 editions of *The Fossil Record*. The overall increase in numbers of families listed, from 2924 to 7186, superficially reflects the effects of new finds and some taxonomic splitting in the intervening 25 years. However, much of the increase is a result of the fact that more groups in 1967 were covered at ordinal level than in the present volume. Also, of course, in many cases, families have been lost as a result of taxonomic revisions.

Hence, there has been a particular advance in the coverage of the sponges, molluscs, annelids, arthropods (especially insects, chelicerates and crustaceans), brachiopods, bryozoans, echinoderms, conodonts, vertebrates and angiosperms. Much of the increase in taxon numbers within these groups has been the result of the more consistent effort to identify families in 1992 than in 1967. However, for some groups, such as insects, chelicerates, teleosts and angiosperms, detailed documentation had not been attempted previously in the way presented here. The composition of family lists for certain groups has also been heavily affected by the introduction of a cladistic methodology. Classifications of vertebrates and of some major groups of sponges, gastropods, arthropods, echinoderms and angiosperms in the present work are wholly, or largely, cladistic. This should mean that most, or all, taxa listed in those chapters are monophyletic; further details are given in individual chapter introductions.

Features of *The Fossil Record 2* (1993) that represent advances over the 1967 version include, in summary:

1. consistent family-level coverage for all groups, except Monera;
2. consistent coverage to the stratigraphical stage level for most records, epoch level for most Precambrian, Cambrian, Ordovician, Silurian, Carboniferous, Miocene and Pliocene, records. For some groups, such as ammonoids, substage designations are given;
3. presentation of 'Intervening' data for many groups;
4. standardized presentation of details for 'First' and 'Last' records;
5. monophyletic, cladistically determined, families within many groups.

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