

BIOHORIZONS AND ZONULES: INTRA-SUBZONAL UNITS IN JURASSIC AMMONITE STRATIGRAPHY

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ABSTRACT. Intra-subzonal units, known collectively as 'horizons', are employed in Jurassic ammonite stratigraphy. Two basic types of 'horizon' are used by different authors. In France the unit is commonly employed as a sub-subzonal division which can be termed a 'zonule'. In Britain and Germany, however, the intra-subzonal unit typically used is more closely comparable to a faunal event. These faunal or 'biohorizons' are analogous to the hemerae of S. S. Buckman. Zonules, therefore, have a significant time duration, whereas biohorizons have a negligible duration but typically a significant inter-biohorizon time interval. As intra-subzonal units 'horizons' offer the potential for much finer scale correlation of marine Jurassic successions than is possible by any other means. The average zonule duration or biohorizon-plus-gap duration currently possible for the British Jurassic is around 200000 years. Nevertheless, calculations of average duration on a stage by stage basis in the Jurassic suggest that at some levels this figure may be as little as 80000 years.

In Jurassic chronostratigraphy, a system of chronozones derived from ammonite biozones is used very effectively for correlation purposes. These 'Standard Zones' are discussed fully by Callomon (1965, 1985*b*) and Callomon and Donovan (1974) and their division into subzones is a result largely of historical considerations (the creation of new subzones within existing zones achieves a degree of nomenclatural stability at zonal level).

Jurassic ammonite stratigraphy has now developed beyond the level of subzones to yet smaller divisions known generally as 'horizons'. The origins of the concept of horizons lie essentially in the *hemerae* of S. S. Buckman (1893, 1902). Buckman (1893, p. 479) noted that 'Ammonites have been chosen as the indicators of horizons [in a general sense] and their rapidity in development makes them peculiarly suitable. Therefore, as far as possible, the chronological unit and the ammonite species should go together.'

Buckman had worked on the Middle Jurassic limestones of the Inferior Oolite Group (Aalenian, Bajocian and lowest Bathonian stages) in Dorset and south Somerset and, through very careful layer by layer ammonite collecting, established a very detailed faunal sequence (Buckman 1893). The Inferior Oolite sequence is, however, highly condensed in this area and no one locality contained a complete faunal succession. Many locally developed non-successes are present and only by considerable cross-correlation was it possible for Buckman to reconstruct a more complete sequence. He realized that the local successions were full of stratigraphical gaps and that each layer with a distinctive ammonite fauna was actually, or probably, separated from others by a time-gap of unknown duration. Each ammonite-bearing layer therefore represented a discrete package of sediment formed during a very short period of geological time.

To use these faunas as correlation tools Buckman (1893, p. 481) created the concept of the 'hemera', taking the name from a Greek word meaning 'day' or 'time'. Each useful fauna from his sequence he identified as belonging to a distinct hemera noting (Buckman 1893, p. 481) that 'successive hemera [*sic*] should mark the smallest consecutive divisions which the sequence of different species enables us to separate in the maximum development of strata.' Unfortunately, however, Buckman managed to discredit much of his early work when he started to derive hypothetically and sometimes inaccurately (e.g. Buckman 1909–1930) hemeral sequences for other parts of the Jurassic.

In the 1920s and 1930s the study of more complete stratigraphical successions than the Inferior Oolite enabled an analogous sequence of small correlative units to be developed by W. D. Lang and

L. F. Spath, for the Lower Jurassic of the Dorset coast (Lang *et al.* 1923, 1928; Lang and Spath 1926). Variably termed 'zones' or 'horizons', these divisions were recognized by the restricted vertical ranges of various nominal ammonite taxa within mudrock-dominated successions of the Lower Lias Group (Hettangian to Lower Pliensbachian stages). Unlike Buckman's hemerae, the small divisions of Lang and Spath formed a continuous stratigraphical sequence with no gaps or overlaps and were therefore effectively rock units, and not time units like hemerae. Later workers, however, such as Spath (1942) and Dean *et al.* (1961), grouped these locally recognizable divisions into larger and stratigraphical coarser units of wider geographical applicability.

The potential to recognize finer correlative divisions than established standard zones and subzones would allow was, however, still recognized. For instance, Callomon (1963, p. 44), in a discussion of the Lower Pliensbachian genera *Liparoceras* and *Beaniceras*, described four successive and clearly distinguishable faunas. These were separated formally as 'Horizons' I to IV. As units identified by discrete faunas, Callomon's horizons were therefore analogous to Buckman's hemerae.

Subsequent development of horizons as intra-subzonal units has, however, been primarily as sub-subzonal units closest to 'conventional' zones and subzones (i.e. very similar to the units used by Lang and Spath for the early Jurassic). This work has been pursued primarily in France and examples are included in Mouterde *et al.* (1970), Cariou (1985) and Corna (1987). Phelps (1985) employed the name *zonule* to distinguish this type of sub-subzonal unit, a term defined by Hedberg (1976) as the smallest division of a chronostratigraphical scale (although the term itself was originally proposed by Fenton and Fenton 1928).

Units analogous to those proposed by Buckman (1893, 1902) have also been used periodically, but often only for specific correlatable faunas within a more conventional zonal sequence (for instance by Callomon 1963 and Callomon and Sykes 1975). It is only relatively recently, however, that this type of unit has once again been used to construct complete correlative sequences. Typically referred to as 'faunal horizons' or 'biohorizons', their use is discussed by Callomon (1985a) and Page (1992) and several schemes are now available for stages or substages of the Jurassic (e.g. Callomon *et al.* 1989; Callomon and Chandler 1990; Dommergues *et al.* 1994).

THE NOMENCLATURE AND CHARACTER OF 'HORIZONS'

As discussed above, 'horizons', as quoted in Jurassic ammonite stratigraphy, belong to two basic types:

Biohorizon (= '*Faunal Horizon*'). A bed or series of beds characterized by a fossil assemblage within which no further stratigraphical differentiation of the fauna (or flora) can be made (Callomon 1985a), i.e. a biohorizon is effectively defined at both its base and top in a single reference section. Callomon (1985a) suggested that the time equivalent of the chronostratigraphical division of biohorizon could be 'hemera' (this is fully compatible with Buckman's earlier usage of that term). The term biohorizon is preferred here to 'faunal horizon' or simply 'horizon' as its meaning is less potentially ambiguous.

Zonule. The smallest component sub-division of a chronostratigraphical hierarchy, defined, as with higher divisions, by a basal boundary stratotype. The term was first applied to standard zonal ammonite stratigraphy by Phelps (1985). Whereas biohorizons tend to be more locally recognizable, Phelps (1985, p. 342) suggested that a sequence of zonules should ideally be useable throughout a palaeobiogeographical province, as are standard zones and subzones.

Biohorizons obviously, therefore, have a number of properties which make them different from conventional chronostratigraphical units, as already noted by Page (1992, p. 134):

1. The recognition of a *biohorizon* is intimately related to the identification of the index *transient species*. A transient is equivalent to a sub-chronospecies, the smallest distinguishable segment of a continuously evolving lineage. Similarly, a biohorizon is the smallest palaeontologically correlatable

segment of geological time. Only the occurrence of diagnostic transient species can confirm the presence of a particular biohorizon, but the general generic or specific composition of a fauna can be a useful guide to recognition.

2. Biohorizons represent discrete but typically very short intervals of geological time, the actual duration of which is not known but is identical to and varies with the times taken to deposit the various defined fauna-containing beds.

3. As the boundaries of most successive biohorizons are not coincident, a significant time gap is potentially present and is shown as an interval between successive units on any correlation diagram.

4. A sequence of biohorizons is established by first constructing a succession of faunal assemblages, and then distinguishing geographically persistent or morphologically distinct associations. These faunas can then form the basis for a defined sequence of biohorizons.

5. Once established, the sequence of defined biohorizons can be integrated with the existing scheme of standard subzones. Nevertheless, the current state of stratigraphical knowledge inevitably means that a subzone may: (a), contain no defined biohorizons; (b), be, for practical purposes, more or less equivalent to a single biohorizon; (c), contain one or more biohorizons, the base of the lowest defining the base of the subzone; or (d), contain one or more biohorizons which may be demonstrably younger than the defined base of the subzone.

6. Biohorizons are usually named in a dual manner, firstly by consecutive numbering and secondly by selecting a suitable transient species as an index.

CORRELATING BIOHORIZONS, AND THE LINK WITH ZONULES

Correlation between different biohorizon schemes is more exacting than the correlation between standard zonal schemes in that:

1. Both the bases *and* tops of each biohorizon can be correlated.

2. The intervals between biohorizons can be as important in correlation as the biohorizons themselves. They may also be correlatable in the same way as biohorizons.

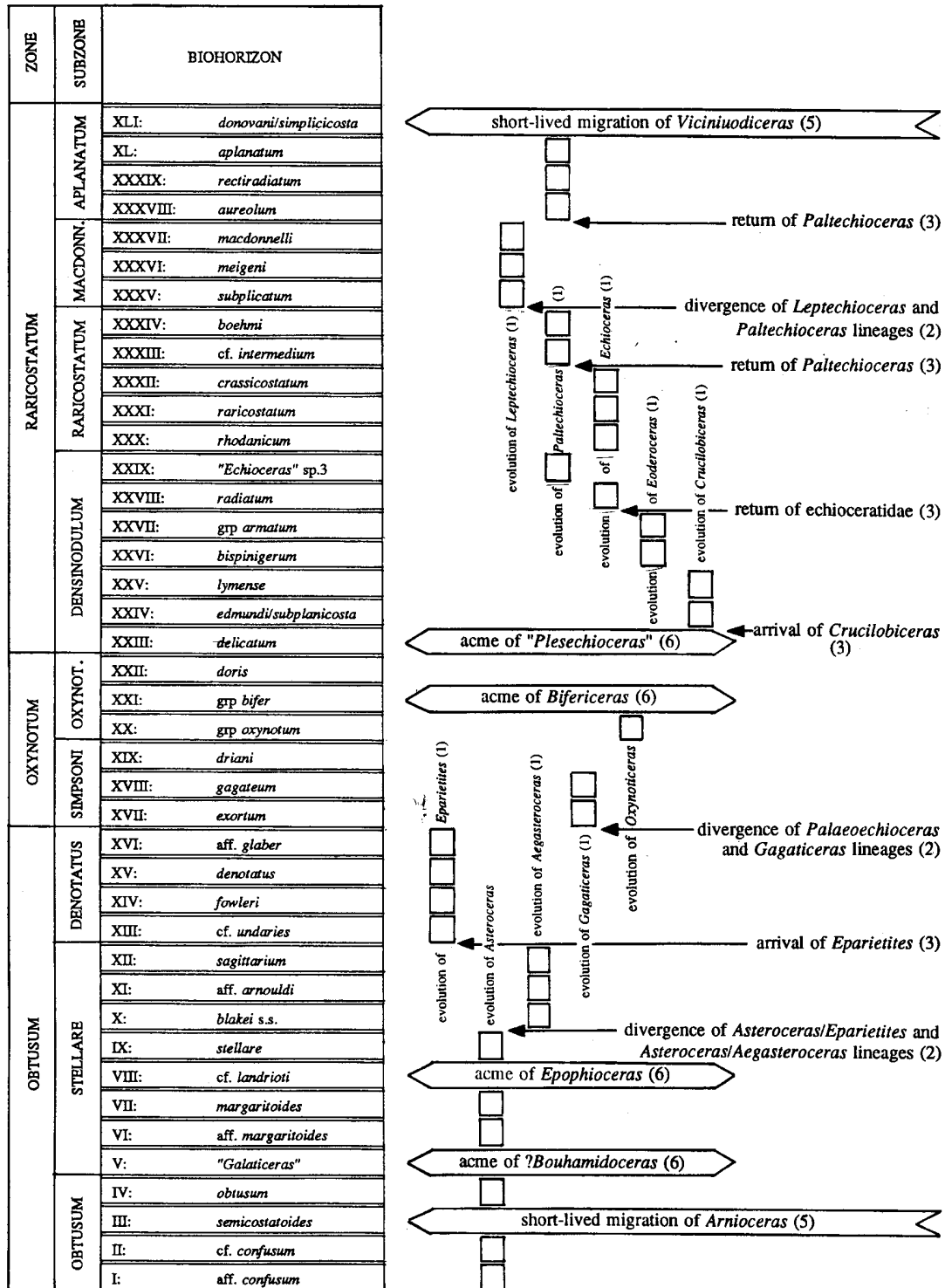
3. A biohorizon can be correlated exactly with another by linking their bases and tops. In other instances, however, the correlated unit may be a biohorizon *plus* the interval below and/or the interval above, or even a sequence of biohorizons (which would inevitably include one or more intervals in the correlation).

4. Following on from the above, every line on the correlation diagram has a very specific meaning and may require some discussion in accompanying text; this is the approach followed by Dommergues *et al.* (1994).

5. Exactly correlated biohorizons (e.g. with linked bases and tops) form, to all intents and purposes, time planes, and can be considered as being equivalent to events in event stratigraphy (Callomon 1985a; Page 1992). These faunal events can form extremely valuable inter-regional correlative datums.

The great value of the construction of a sequence of biohorizons is that it effectively defines the observed succession of faunas. As noted by Buckman (1893, p. 481), it is this detailed basic information on faunal sequences which is so important to any future work: '... it may be remarked that the more minute the correlation the better for the student; he can easily dispense with detail; but if such detail as he does need be not given in any paper, he searches in vain for information.' Unfortunately it is this basic information that is so often lacking in many classical works and the contractions of the faunal sequence that are zones and subzones are quoted in discussions of stratigraphy, phylogeny and evolution as though they are the ultimate in resolvable chronology.

Intra-regional or international correlation of biohorizon sequences will establish those units suitable to form the basis for the definitions of a sequence of zonules. As noted previously, zonules should ideally be recognizable throughout a palaeobiogeographical province, as are subzones. The creation of new sub-divisions of existing sequences of standard subzones at the level of zonules helps maintain a degree of nomenclature stability, by removing the necessity to tamper with familiar zonal



TEXT-FIG. 1. For legend see opposite.

and subzonal names and successions in order to achieve an increase in potential correlative resolution. Each defined zonule could contain one or more biohorizons, one of which may or may not be coincident with its defined base (identical to the biohorizon/subzonal relationship described above).

THE NATURE OF BIOHORIZONS

It is a remarkable feature of many biohorizons just how widely geographically they can be recognized. For instance, the basal Callovian *keppleri* Horizon of Callomon *et al.* (1989), characterized by the kosmoceratid *Kepplerites keppleri* (Oppel) is recognizable in southern England, Germany, Switzerland and also Georgia and East Greenland. The *keppleri* Horizon is an extreme example but several other biohorizons in the Lower Callovian are also recognizable in Britain and Germany (Callomon *et al.* 1989; Mönning 1989), and Britain, south-eastern and eastern France have many Sinemurian biohorizons in common (Dommergues *et al.* 1994).

As noted by Mettraux *et al.* (1992) there is an interplay of supra-regional, regional and local processes underlying these distributions, but it is not always possible to determine readily exact causes. Biological, sedimentological and tectonic effects are involved, but although potential factors may be diverse, a number of key processes appear to facilitate the recognition of most biohorizons. These key processes or factors are:

1. The evolution of one or more ammonite populations/lineages within the biogeographical province under study, leading to the development of distinguishable transients (i.e. sub-chronospecies).

2. The evolution and divergence of related ammonite populations within the basin or province under study (e.g. branching of a lineage or 'true' speciation).

3. The evolution of an ammonite lineage (e.g. genus) present in the province under study, in an adjacent province (or a separated area of the same province), followed by the migration of the new form into the study area (with or without the survival of the local, related population).

4. The presence of morphologically complex and 'rapidly evolving' groups. It is easier to characterize small changes in successive populations of highly ornamented genera than it is to separate successive faunas of morphologically 'simpler' groups. As a consequence, highly ornamented genera will tend to have more distinguishable transients over a given stratigraphical interval than relatively morphologically simpler genera, and therefore will facilitate the recognition of a greater number of biohorizons.

5. The migration into the area being studied, from another basin or province, of a 'new' ammonite population/lineage (i.e. a lineage not present in the immediately preceding biohorizon). This migration may be short-lived (e.g. one transient/biohorizon duration) or may lead to the establishment of a 'local', possibly evolving, population (e.g. surviving for one or more biohorizons).

6. Changes in faunal composition including 'acme-events' (including dominance) of certain lineages, presumably resulting usually from environmental or ecological changes.

7. The periodical or occasional preservation of suitable ammonite faunas resulting from fluctuating or cyclic sedimentary processes, e.g. due to turbiditic sedimentation or Milankovitch cycle-driven sedimentary rhythms.

It is the action of ecological, sedimentological and tectonic controls which preserve snapshots of the basic underlying evolutionary processes listed first above (factors 1–4). The most common and typical combined factors facilitating the recognition and correlation of biohorizons are:

- (a). The morphological evolution of an ammonite population in the basin/province under study and the periodical preservation of faunas, thereby leading to the easy separation of successive

TEXT-FIG. 1. Diagnostic faunal events underlying the identification of Upper Sinemurian biohorizons in Britain (N.B. complete ranges of taxa not shown). The biohorizonal scheme is that of Dommergues *et al.* (1994). Bracketed numbers indicate the nature of the 'event' or process as described in the text under 'The Nature of Biohorizons'.

Stage/Substage		Duration after Harland et al	Zonal Divisions in Britain	Horizons, etc: Britain		Zonal Divisions in France	Zonules, etc: France	
				No. of Potential Divisions	Average Duration		No. of Potential Divisions	Average Duration
Tithonian	Portlandian/Volgian	6.5	11 SB	13 SB	210,000 years	9 SM	9 SM	722,000 years
	Upper Kimmeridgian		11 SB	18 SB		11 7SB	27 7SB	
	Lower Kimmeridgian	2.6	5 SB	17 SB	153,000	8 SM	12 SM	80,000
	Upper Oxfordian	2.4	7B	11B	90,000	6 SM	9 SM	
	Middle Oxfordian		4B	7B		5 SM	9 SM	
	Lower Oxfordian		5 SB/B	8 SB		4 SM	10 SM	135,000
	Upper Callovian	4.2	5 SB	9 SB	5 SM	10 SM		
	Middle Callovian		4 SB	7 SB	7 SM	11 SM		
	Lower Callovian		8 SB	19 SB	6 SM	8 SM	267,000	
	Upper Bathonian	4.8	4 SB	5 SB	4 SM	6 SM		
	Middle Bathonian		3 SB	5 SB	4 SM	4 SM		
	Lower Bathonian		4 SB	4 SB	6 SM	10 NW	352,000	
	Upper Bajocian	7.4	8 NW	9 NW	9 NW	11 NW		
	Lower Bajocian		8 NW	19 NW	8 NW	16 NW	281,000	
	Aalenian	4.5	9 NW	16 NW	281,000	13 NW	17 NW	310,000
	Upper Toarcian	9	7 NW	11 NW	290,000	6 NW	12 NW	
	Lower Toarcian		9 NW	20 NW		5 NW	18 NW	188,000
	Upper Pliensbachian	7.5	5 NW	10 NW	214,000	10 NW	22 NW	
	Lower Pliensbachian		10 NW	25 NW		9 NW	41 NW	155,000
	Upper Sinemurian	9	9 NW	41 NW	120,000	8 NW	17 NW	
	Lower Sinemurian		8 NW	34 NW		6 NW	12 NW	375,000
	Hettangian	4.5	6 NW	18 NW	250,000			

TEXT-FIG. 2. For legend see opposite.

transients (i.e. morphological intermediates between observed transients are absent or rare because of non-preservation).

(b). The migration of a 'new' ammonite population into the basin/province under study as a result of the removal of barriers to migration. Migration may be short-lived or may lead to long or short-term establishment of a resident population which evolves and is preserved as above.

As an example of evolutionary and ecological factors in operation, Text-figure 1 shows the Upper Sinemurian biohorizonal sequence proposed by Dommergues *et al.* (1994) interpreted in terms of the key faunal events which facilitate the recognition and correlation of each biohorizon in Britain.

Dommergues and Meister (1991) have further investigated the frequency with which late Sinemurian and early Pliensbachian biohorizons could be recognized in a broader North-West European context and observed phases in which biohorizons were recognizable primarily at basin margins and phases when a basin centre distribution was more apparent. Concluding, Dommergues and Meister (1991, p. 978) noted that factors such as sea-level change, taphonomy and ecological considerations may be controlling these distributions and speculated that 'the comparison with sequence stratigraphy can probably be a valid research program in the future.'

THE DURATION OF HORIZONS

As intra-subzonal units, the average duration of zonules and the average biohorizon-plus-interval duration, must be, geologically speaking, very short. Callomon (1985a) estimated an average figure for this in the Jurassic of 120000 years, based on a general estimation of the number of horizons the system could potentially contain.

There are two great problems with such estimations: firstly, biohorizon and zonule schemes are only available for relatively few stages; and secondly, the available radiometric time scales are relatively crude. The Harland *et al.* (1990) time scale provides a 'standard' framework for estimating the duration and interval length, but tie-points linking radiometric ages directly to the chronostratigraphical scale are few and only five could be used by Harland *et al.* (1990) for the Jurassic, namely at the Tithonian/Berriasian (i.e. Tethyan Jurassic/Cretaceous) boundary (145 Ma), the Kimmeridgian/Oxfordian boundary (153.5 Ma), in the 'mid Bajocian' (168.2 Ma), at the Sinemurian/Hettangian boundary (203.5 Ma) and at the Rhaetian/Norian boundary (within the Upper Triassic; 210.5 Ma). The net result is that stage length and even the position of the base of the Jurassic are frequently 'guestimated' using an averaged figure for the duration of standard ammonite zones. This is obviously highly unsatisfactory and one can only await the development of better Jurassic time-scales. Nevertheless, taking the Harland *et al.* (1990) figures for stage duration as a 'standard' for comparison one can attempt to get some idea of potential relative stratigraphical resolution for each of the Jurassic stages.

TEXT-FIG. 2. Number of conventional zonal divisions (mainly subzones) compared with actual or potential minimum number of horizons for Jurassic stages and substages in Britain and France (see discussion in text). Estimated average zonule duration or inter-biohorizon interval shown. Abbreviations of faunal provinces: NW = North-West European Province; SM = Sub-Mediterranean Province; SB = Sub-Boreal Province; B = Boreal Province. Sources of information as follows: Hettangian – Lang (1924), Donovan (1956), Whittaker and Green (1983), Bloos (1985), Mouterde and Corna (1991), pers. obs.; Sinemurian – Corna (1987), Corna *et al.* (1991), Page (1992), Dommergues *et al.* (1994), pers. obs.; Pliensbachian – Lang (1928), Howarth (1955, 1956, 1957), Dommergues (1979), Phelps (1985), Dommergues *et al.* (1991). Toarcian – Dean (1952), Howarth (1962, 1973, 1978), Elmi *et al.* (1991), pers. obs.; Aalenian – Contini (1969), Callomon and Chandler (1990), Contini *et al.* (1991b). Bajocian – Callomon and Chandler (1990) with later additions for Upper Bajocian (unpublished enclosure with reprints), Contini *et al.* (1991a); Bathonian – Arkell (1951–1959), Torrens (1974, 1980), Dietl and Callomon (1988), Westermann and Callomon (1988), Mangold (1991); Callovian – Callomon (1968), Cariou (1985), Callomon *et al.* (1989), Thierry *et al.* (1991), pers. obs.; Oxfordian – Arkell (1935–1948), Sykes and Callomon (1979), Callomon (1989), Cariou *et al.* (1991); Kimmeridgian – Birkelund *et al.* (1983), Hantzpergue (1989), Hantzpergue *et al.* (1991); Tithonian – Cope (1967, 1978), Casey (1973), Wimbledon (1984), Geysant and Enay (1991).

The first problem, relating to the number of 'horizons' in each Jurassic stage, is similarly unresolved. It is straightforward to calculate average durations when published schemes are available, but is obviously more problematical when these have not yet been derived. It is, nevertheless, possible to construct provisional biohorizon sequences when detailed stratigraphical descriptions are available for key ammonite-rich successions. By using such descriptions and deducing a sequence of distinguishable faunas a crude estimate of the *minimum* number of potential biohorizons can be gained.

Using the Harland *et al.* (1990) 'standard' for stage duration in years, and the figures (actual and estimated) for biohorizon or zonule number in each stage, Text-figure 2 has been constructed. This shows the relationship between the resolution available for each substage or stage with conventional zonal units (essentially subzones) and with horizons, as numbers of each unit potentially available. The possible average duration or interval length of each actual or potential horizon sequence is then given (assuming that the Harland *et al.* time scale is close to reality). British and French sequences are compared.

It will be noticed immediately that the calculated biohorizon-plus-interval or zonule duration varies greatly, between a very short 80000 years in the French Oxfordian to a much cruder 722000 years in the French Tithonian. Figures around 200000–350000 years are more typical.

A second and probably more meaningful way of looking at these figures is to attempt an estimation of average duration using the Harland *et al.* (1990) dating of tie-points as a guide. The result is as follows:

Interval	Interval duration	Estimated minimum number of 'horizons'	Average duration of zonule or biohorizon-plus-gap
Base of Kimmeridgian to top of Tithonian	8.5 My	48 (GB) 26 (Fr.)	177000 yrs (GB) 327000 yrs (Fr.)
'Mid' Bajocian to top of Oxfordian	14.7 My	84 (GB) 89 (Fr.)	175000 (GB) 165000 (Fr.)
Base of Sinemurian to 'Mid' Bajocian	35.3 My	175 (GB) 154 (Fr.)	202000 (GB) 229000 (Fr.)
Base of Rhaetian (Triassic) to top Hettangian	7.0 My	18+4 (GB) 13+4 (Fr.)	318000 (GB) 412000 (Fr.)

Notes: 1, For convenience the 'Mid' Bajocian tie-point of Harland *et al.* (1990) is taken as corresponding with the Lower/Upper Bajocian boundary; 2, in the virtual absence of latest Triassic ammonoids in Britain and France, a figure of four is used for the correlation resolution of the Rhaetic Stage, derived from the zonation of that stage in southern Europe (Tethyan Realm) of Wiedman *et al.* (1979).

These figures are likely to be more accurate values for average horizon durations and intervals than those of Text-figure 2, but many are certainly still too high as only a minimum value for horizon number is derivable for stages or substages where published schemes do not exist.

Whichever of these, or indeed any other, figures one chooses to use for average biohorizon-plus-interval or zonule duration, there is no doubt that the use of these units can increase greatly the potential resolution of correlation of marine Jurassic sequences. No other correlation method can offer this level of resolution, and certainly not over large distances. Horizons have a real potential to revolutionize all aspects of Jurassic stratigraphical practice and are certainly far more valuable to non-ammonite specialists than is perhaps currently recognized.

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APPENDIX: PUBLISHED BRITISH HORIZONTAL SCHEMES

SUBSTAGE	ZONE	SUBZONE	BIOHORIZON		
LOWER SINEMURIAN	TURNERI	BIRCHI	31: <i>cf. bordoti</i>		
			30: <i>subturneri</i>		
			29: <i>birchi</i>		
			28: <i>pseudobonnardi</i>		
			27: <i>obtusiformis</i>		
			26: <i>hartmanni</i>		
		BROOKI	25: <i>brooki</i>		
			24: <i>sulcifer</i>		
			SEMICOSTATUM	RESUPINATUM	23: <i>cf. semicostatum</i>
					22: <i>alcinoeiforme</i>
					21: <i>Euagasiceras</i>
				SCIPIONANUM	20: <i>cf. resupinatum</i>
	19: <i>pseudokridion</i>				
	18: <i>acuticarinatum</i>				
	LYRA	17: <i>Paracoroniceras</i>			
		16: <i>bodleyi</i>			
		15: <i>lyra</i>			
		BUCKLANDI	14: <i>multicostatum</i>		
			13: <i>cf. scunthorpense</i>		
			12: <i>isis</i>		
	11: <i>aff. isis</i>				
	BUCKLANDI		ROTIFORME	10: <i>scylla</i>	
				9: <i>kridion</i>	
		8: <i>caprotinum</i>			
		CONYBEARI	7b: <i>aff. rotiforme</i>		
			7a: <i>rotiforme</i>		
			6: <i>cf. defneri</i>		
	5: <i>conybeari</i>				
	4: <i>cf. rotator</i>				
	3b: <i>rouvillei</i>				
	3a: <i>rotarium</i>				
	2b: <i>Metophioceras</i> sp. 2				
	2a: <i>Metophioceras</i> sp. 1				
1: <i>cf. rougemonti</i>					

TEXT-FIG. 3. Lower Sinemurian Biohorizons (modified from Page 1992).

SUBSTAGE	ZONE	SUBZONE	BIOHORIZON		
UPPER SINEMURIAN	RARI-COSTATUM	APLANATUM	XLI: <i>donovani/simplicicosta</i>		
			XL: <i>aplanatum</i>		
			XXXIX: <i>rectiradiatum</i>		
			XXXVIII: <i>aureolum</i>		
			XXXVII: <i>macdonnelli</i>		
			XXXVI: <i>metgeri</i>		
		RARI-COSTATUM	MACDONN.	XXXV: <i>subplicatum</i>	
				XXXIV: <i>boehmi</i>	
				XXXIII: <i>cf. intermedium</i>	
				XXXII: <i>crassicostatum</i>	
				XXXI: <i>rari-costatum</i>	
				XXX: <i>rhodanicum</i>	
		DENSINODULUM	RARI-COSTATUM	XXIX: <i>"Echioceras" sp.3</i>	
				XXVIII: <i>radiatum</i>	
				XXVII: <i>grp armatum</i>	
				XXVI: <i>bispinigerum</i>	
				XXV: <i>lymense</i>	
				XXIV: <i>edmundi/subplanicosta</i>	
	XXIII: <i>delicatum</i>				
	OXYNOTUM			OXYNOT.	XXII: <i>doris</i>
					XXI: <i>grp bifur</i>
					XX: <i>grp oxynotum</i>
					XIX: <i>driani</i>
					XVIII: <i>gagateum</i>
		XVII: <i>exortium</i>			
	OBTUSUM	DENOTATUS	XVI: <i>aff. glaber</i>		
			XV: <i>denotatus</i>		
			XIV: <i>fowleri</i>		
			XIII: <i>cf. undaries</i>		
			XII: <i>sagittarium</i>		
			XI: <i>aff. arnouldi</i>		
		STELLARE	OBTUSUM	X: <i>blakei s.s.</i>	
				IX: <i>stellare</i>	
				VIII: <i>cf. landrioti</i>	
				VII: <i>margaritoides</i>	
				VI: <i>aff. margaritoides</i>	
				V: <i>"Galaticeras"</i>	
	OBTUSUM	OBTUSUM	IV: <i>obtusum</i>		
			III: <i>semicostatoides</i>		
			II: <i>cf. confusum</i>		
			I: <i>aff. confusum</i>		

TEXT-FIG. 4. Upper Sinemurian Biohorizons (from Dommergues *et al.* 1994).

SUBSTAGE		ZONE		SUBZONE	ZONULE				
DOMERIAN (pt.)		MARGARITATUS (pt.)							
CARDUKIAN (pt.)	IBEX	MASSSEANUM	MURCHISONAE	SUB-ODOSUS					
						VALDANI	STOKESI	Wertheri	Celebratum
									Nitescens
		Monestieri							
		LURIDUM	CAPRICORNUS	FIGULINUM		Bifurcatus	Occidentale		
							Lepidum		
	Crassum								
	MURCHISONAE	MURCHISONAE	MURCHISONAE	MURCHISONAE	Rotundum				
					Centaurus				
					Centaurus				
	MURCHISONAE	MURCHISONAE	MURCHISONAE	MURCHISONAE	Actaeon				
					Venarense				
Valdani									
MURCHISONAE	MURCHISONAE	MURCHISONAE	MURCHISONAE	Maugenesti					
				Arietiforme					
				Masseanum					
JAMESONI	JAMESONI	JAMESONI	JAMESONI	JAMESONI					

TEXT-FIG. 5. 'Mid' Pliensbachian Zonules (after Phelps 1985).

STAGE		ZONE		SUBZONE	BIOHORIZON	
AALENIAN		CONCAVUM				
AALENIAN	MURCHISONAE	HAUJOBTUSI	MURCHISONAE	CONCAVUM	Aa-16: <i>acanthodes</i>	
					Aa-15: <i>formosum</i>	
					Aa-14: <i>concauum</i>	
					Aa-13: <i>cavatum</i>	
		BRADFORDENSIS	BRADFORDENSIS	GIGANTEA	CONCAVUM	Aa-12: <i>decipiens</i>
						Aa-11: <i>gigantea</i>
						Aa-10: <i>bradfordensis-similis</i>
						Aa-9: <i>bradfordensis-baylii</i>
	SCISSUM	MURCHISONAE	MURCHISONAE	CONCAVUM	Aa-8: <i>bradfordensis-subcornuta</i>	
					Aa-7: <i>murchisonae</i>	
					Aa-6: <i>patellaria</i>	
					Aa-5: <i>obtusiformis</i>	
					Aa-4: <i>opalinoides</i>	
					Aa-3: <i>bifidatum</i>	
					Aa-2: <i>lineatum</i>	
					Aa-1: <i>opalinum</i>	

TEXT-FIG. 6. Aalenian Biohorizons (after Callomon and Chandler 1990). Abbreviations: Opalin. = Opalinum; Obtusi. = Obtusiformis.

SUBSTAGE		ZONE	SUBZONE	BIOHORIZON
UPPER BAJOCIAN				
SUBBURCÁTUM	GABARTIANA	PARKL- NISONI	Bj-28:	<i>bomfordi</i>
			Bj-27:	<i>truelli</i>
			Bj-26:	<i>acris</i>
			Bj-25:	<i>tetragona</i>
			Bj-24:	<i>garartiana</i>
	BANKSI	POL-BAC- GAR- TET- ACR- TRU- BOM- FOR	Bj-23:	<i>davidsoni</i>
			Bj-22:	<i>polygyralis</i>
			Bj-21:	<i>aplous</i>
			Bj-20:	<i>banksi</i>
			Bj-19:	<i>coronatum</i>
LOWER BAJOCIAN				
HUMPHRIESIANUM	CYC- LOI-	HOMPHRE- SIANUM	Bj-18:	<i>blagdeni</i>
			Bj-17:	<i>blagdeniforme</i>
			Bj-16:	<i>gibbosum</i>
			Bj-15:	<i>humphriesianum</i>
			Bj-14:	<i>cycloides</i>
	SAUZEI	BLAG- DENI	Bj-13:	<i>umbilicatum</i>
			Bj-12:	<i>rhyium</i>
			Bj-11:	<i>sauzei</i>
			Bj-10:	<i>laeviuscula</i>
			Bj-9:	<i>ruber</i>
LAEVUSCULA	TRIGO- NALIS	Bj-8:	<i>trigonalis</i>	
		Bj-7:	<i>connata</i>	
		Bj-6:	<i>'ovalis'</i>	
OVALIS	LAEVI- USCULA	Bj-5:	<i>romanoides</i>	
		Bj-4:	<i>inclusa</i>	
		Bj-3:	<i>subsectum</i>	
DISCITES	KEPPLERI- TEREBRATUS	Bj-2b:	<i>rudidiscites</i>	
		Bj-2a:	<i>walkeri</i>	
		Bj-1:	<i>politum</i>	

TEXT-FIG. 7. Bajocian Biohorizons (after Callomon and Chandler 1990, with later additions for Upper Bajocian). Abbreviations: Bacula. = Baculata; Bomfo. = Bomfordi; Cycloi. = Cycloides; Garant. = Garantiana; Polygy. = Polygyralis; Tetrag. = Tetragona; Truel. = Truelli.

SUBSTAGE		ZONE	SUBZONE	BIOHORIZON
LOWER CALLOVIAN				
HERVEVI	KAMPTUS	GOWER- IANUS	VII:	<i>polypychus</i>
			VI:	<i>kamptus</i> B
			V:	<i>kamptus</i> α
			IVb:	<i>terebratus</i> γ
			IVa:	<i>terebratus</i> B
	CURTIOLOBUS	GAL-CALLOV- ILAIENSE	III:	<i>galilaei</i>
			XII:	<i>tricophorus</i>
			XIb:	<i>indigestus</i>
			XIa:	<i>'gregarium'</i> MS
			X:	<i>curtilobus</i>
CALLOVIENSE				
ENODATUM	GAL-CALLOV- ILAIENSE	XV:	<i>micans</i>	
		XIV:	<i>calloviense</i>	
		XVI:	<i>enodatum</i> α	
		XVIIa:	<i>difficilis</i>	
		XVIIb:	<i>enodatum</i> B	
		XVIII:	<i>anterior</i>	
		I:	<i>keppleri</i>	
		II:	<i>verus</i>	

TEXT-FIG. 8. Lower Callovian Biohorizons (modified from Callomon and Page in Callomon *et al.* 1989). Abbreviation: Galila. = Galilaeii.