History and status of the biomere concept

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Biomeres are Cambrian stage-level, extinction-bounded, trilobite-based biostratigraphic units in the shallow shelf successions of Laurentian North America. Controversy over the placement of biomere boundaries, the claim that diversification within a biomere represents a true adaptive radiation, and the possible cause(s) and phylogenetic significance of the bounding extinctions are all discussed. Background information on some of the prominent palaeontologists who contributed to the debates is included to provide insight to their differing perspectives and potential biases. Recent phylogenetic studies have raised serious doubt regarding the original view of biomeres as phylogenetically unique and coherent units produced by endemic speciation in an effectively closed system on the shelf. Still, the biomere has value as a natural stratigraphic package that records the rise and fall of taxonomic and morphologic diversity within platform faunas between post-extinction minima. At each of the three well documented Upper Cambrian biomere boundaries the minimum-diversity fauna, which appears one or two trilobite subzones above an extinction horizon that serves as a chronostratigraphic stage boundary, is dominated by a generalised genus representing or resembling the Family Olenidae (i.e., an "olenimorph"). Recent studies of biomere boundaries utilising high-resolution sedimentological, biostratigraphic, and geochemical data revealed physical and isotopic evidence consistent with a drop in water temperature and/or oxygen concentration in the extinction interval. This might have been mediated by sea level rise initiated well in advance of the extinction process. However, the evidence of such environmental change is not conclusive.

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THICK SUCCESSIONS of Cambrian and Lower Ordovician strata were preserved in various depocentres in Laurentian North America as a result of rising sea level and rapid subsidence on passive margins created by late Precambrian rifting. Lithologic and faunal contrasts between nearshore clastics, shallow platform carbonates, and off-platform deep water facies allow delineation of Inner Detrital, Middle Carbonate, and Outer Detrital facies belts arranged roughly concentrically around the North American craton (Palmer 1960). Rapid evolution of trilobites within each of these belts produced a faunal succession that facilitates subdivision of the Upper Cambrian and Lower Ordovician into numerous, relatively thin zones and subzones that are useful for correlating rocks of that age and environmental setting throughout North America.

Evolutionary turnover in trilobites was especially rapid during approximately the latter third of the Cambrian, an interval whose deposits compose what are now known (Palmer 1998) as the Lincolnian and Millardan Series (Fig. 1). The three highest stages of the Cambrian are bounded by widely correlatable extinction horizons that record the decimation of diverse shallow marine trilobite faunas and subsequent immigration of genera from deeper outer-shelf or off-shelf environments. However, each stadial boundary marks the beginning, rather than the end of the extinction/replacement process. The basal strata of the overlying stage constitute a 'critical interval', spanning one or two thin trilobite subzones, that contains a fauna that is much reduced in diversity but is still dominated by a species or genus from the pre-extinction fauna of the underlying stage. Few, if any, of these survivors occur in the replacement fauna that appears immediately above the critical interval. Instead, the replacement fauna is dominated by a generalised ptychopariid genus whose features resemble those that characterise the Family Olenidae. Fortey & Owens (1990) coined the term "olenimorph" to describe such trilobites. The zonal or subzonal boundary marked by the appearance of the olenimorph-dominated replacement fauna (i.e., the top of the critical interval) is a biomere boundary (Taylor 1997; Myrow *et al*. 1999).

Thus defined, a biomere is a stage-level, superzonal biostratigraphic unit that records the rise of shallow marine trilobite faunal diversity

SERIES	STAGE	BIOZONE	BIOMERE
IBEXIAN	Skullrockian	Paraplethopeltis	"Symphysurinid"
		Bellefontia	
		Symphysurina	
		Missisquoia	
MILLARDAN	Sunwaptan	Saukia	Ptychaspid
		Ellipsocephaloides	
		Saratogia	
		Taenicephalus	
	Steptoean	Elvinia	Pterocephaliid
		Dunderbergia	
		Dicanthopyge	
		Aphelaspis	
LINCOLNIAN	Marjuman	Crepicephalus	Marjumiid
		Cedaria	
		Bolaspidella	
		Ehmaniella	
		Glossopleura	

Fig. 1. Relationship of biomeres to upper Cambrian (Lincolnian and Millardan) and basal Ordovician (Ibexian) biozones and stages established for shallow marine strata in North America.

on the Laurentian shelf from a post-extinction minimum to its maximum prior to the onset of the next major extinction, and its decline through the critical interval that followed. Three biomeres in the Upper Cambrian are well-documented. Each is named for a trilobite family whose members are major elements of the constituent faunas. They are (in ascending order) the Marjumiid, Pterocephaliid, and Ptychaspid Biomeres (Fig. 1). Some authors (Palmer 1981; Sundberg 1994) have also identified a 'Corynexochid Biomere' directly below the Marjumiid Biomere, noting the abundance of olenimorphs low in the *Ehmaniella* Zone. Stitt (1983) defined a fourth biomere on data from Lower Ordovician strata in Oklahoma. This 'Symphysurinid Biomere' extends upward from the top of the Ptychaspid Biomere to the extinction horizon at the top of the *Paraplethopeltis* Zone, the boundary recently selected by Ross *et al*. (1997) to define the top of the Skullrockian Stage. However, no evidence has yet been found of an olenimorph-dominated replacement fauna at the base of the overlying Stairsian Stage.

This paper reviews the history of the biomere concept whose development derives from the contributions of many prominent trilobitologists and biostratigraphers over the past four decades. An attempt is made to set the context of each change in the biomere concept in terms of significant directions and developments in the field of palaeontology over that span of time. Stitt (1975, 1977) and Palmer (1984) provided thorough reviews of the concept's history through its first 10-15 years. For that reason, the sections in the present paper that deal with developments through 1984 are fairly brief. Conversely, the discoveries and debates regarding the evolutionary significance of biomeres and potential extinction mechanisms proposed through the late 1980s and 1990s are treated in greater detail. Some information on the background of the individuals who played a significant role in the evolution of the concept is included to provide some insight to their unique perspectives and potential biases.

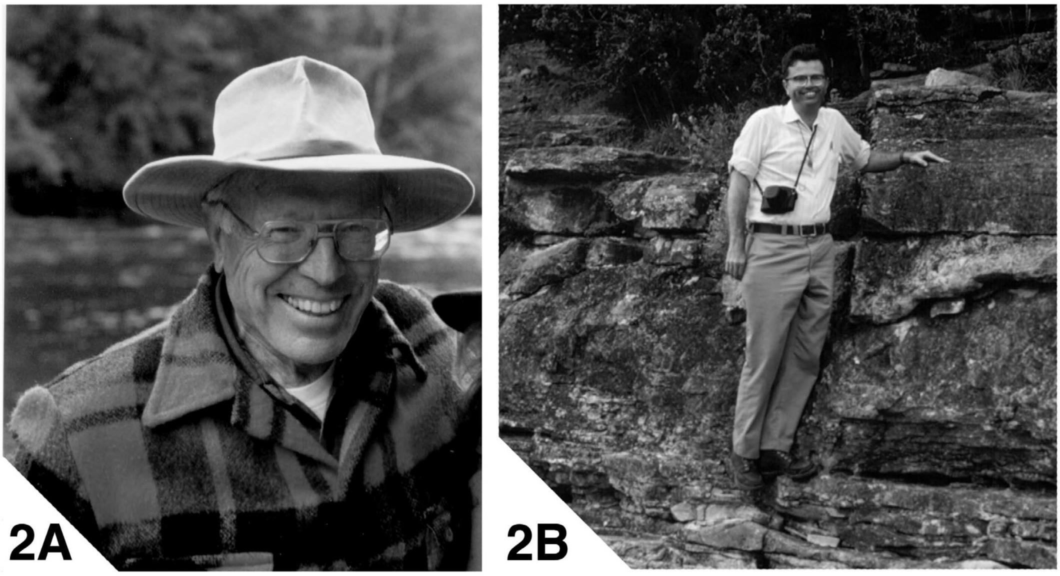

Fig. 2. Primary advocates of the biomere concept in the 1960's and 1970's. A, Allison R. (Pete) Palmer, originator of the biomere. Photo taken by Christian W. Gronau in British Columbia, in September, 1997; B, James H. Stitt, biostratigrapher at University of Missouri who first recognised internal 'stages', including the thin crisis interval (stage 4) at the top of the unit. Photo by James F. Miller in central Texas in the late 1970's.

DEVELOPMENT OF THE CONCEPT

Biomeres Defined (1965-1970)

The biomere concept was introduced at a time when palaeontologic work was focused on development and refinement of a biostratigraphic framework to provide time control for field mappers and other practical geologists engaged in the survey of resources in the United States. The first American Code of Stratigraphic Nomenclature (American Commission on Stratigraphic Nomenclature 1961), which for the first time formally set Biostratigraphic Units apart as a separate category from Lithostratigraphic Units, had just been published. Although biozonal boundaries need not be synchronous surfaces, in practice most biostratigraphers have selected boundaries that approximate time lines to expedite stratigraphic research that relies on biostratigraphy for temporal control. The abundance of papers on trilobite taxonomy and biostratigraphy in the *Journal of Paleontology* through the 1950s and 1960s reflects an emphasis on zonation and correlation.

In contrast, many papers from the 1940s and 1950s in which Cambrian trilobite faunas were described lack stratigraphic control and/or coverage, sometimes due to lack of attention to that aspect, but frequently because of the limitations of exposures available in the northern midcontinent and Appalachian regions. Franco Rasetti, for example, described trilobites from limestone boulders within deep marine conglomerates (olistostromes) in the vicinity of Levis, Quebec (Rasetti 1943, 1944, 1945, 1963) and from isolated exposures of the Upper Cambrian Frederick and Grove Formations in Maryland (Rasetti 1959, 1961). In fact, many of the new genera and species described from the Frederick and Grove Formations were collected from loose blocks in a stone wall near Frederick, Maryland! In contrast, systematic sampling of faunas within superbly exposed Upper Cambrian carbonate platform successions in the western U.S. and Canada eventually allowed development of highly refined trilobite-based zonations (Palmer 1954, 1960, 1965a; Grant 1965; Winston & Nicholls 1967; Stitt 1971a, 1977, 1983; Ludvigsen 1982; Westrop 1986; among others).

Allison R. Palmer (Fig. 2A), who himself can't tell you why his parents dubbed him "Pete" in his early years, introduced the term biomere (Palmer 1965a, b) for a stage-level package of trilobite zones in the thick succession of Upper Cambrian carbonate platform strata of the western United States. Pete Palmer is arguably the most renowned Cambrian specialist in North America, regularly presiding over Friends of the Cambrian meetings held each year at the national meeting of the Geological Society of America and currently serving in 'retirement' as the director of the Institute for Cambrian Studies in Boulder, Colorado. Palmer earned his undergraduate degree in geology in 1946 from Pennsylvania State University where he fell under the influence of F. M. Swartz and elected to pursue a career in palaeontology and stratigraphy. Serendipity and the university's location in the Nittany Valley, an anticlinal valley carved out in weakly resistant lower Palaeozoic carbonates, also played a part in his decision. For lack of a car, his geologic explorations were limited to exposures within walking distance of the Penn State campus. Among the units exposed in the vicinity is the Stonehenge Limestone whose uppermost beds include bioclastic grainstones with abundant trilobite remains. On a student field trip to Bellefonte, Pennsylvania, Palmer cracked off a piece of limestone from that interval and found himself holding an exquisite, completely articulated specimen of the asaphid trilobite *Bellefontia collieana* - and he was hooked. The discovery prompted him to explore exposures near campus where he found another trilobite, this time *Hystricurus*, that Swartz identified as a species not previously reported from the Stonehenge. With encouragement from Swartz, Palmer completed a Senior thesis on the fauna. So somewhat ironically, it was a Lower Ordovician trilobite fauna that directed Pete Palmer's career path into Cambrian biostratigraphy.

Palmer completed his doctorate at the University of Minnesota under W. Charles Bell, one of the most influential biostratigraphers of his time. The magnitude of Charlie Bell's contribution to the refinement of the biostratigraphic framework available for correlation of Cambrian rocks in North America is difficult to overstate when one considers the papers that he himself authored or coauthored (Bell 1941; Bell *et al.* 1952; Bell *et al.* 1956; Bell & Ellinwood 1962; among others), the body of work ultimately produced by graduate students who he supervised at the University of Minnesota (Robert R. Berg, Oliver W. Feniak, Vincent E. Kurtz, Clem A. Nelson and Allison R. Palmer) or the University of Texas (Howard L. Ellinwood, Richard E. Grant, Susan A. Longacre, Harry Nicholls, Richard A. Robison, James H. Stitt, James Lee Wilson and Don Winston), and the accomplishments of their many students.

Although Bell worked primarily with brachiopods, most theses and dissertations conducted under his supervision dealt more with trilobites. Pete Palmer's dissertation on the Riley Formation in central Texas was no exception. In that study, which he refined and published in a now classic paper (Palmer 1954) shortly after joining the U.S. Geological Survey, Palmer documented the stark contrast between the diverse fauna of the *Crepicephalus* Zone and the austere trilobite assemblage of the overlying *Aphelaspis* Zone. As subsequent work with the survey led him to describe progressively younger faunas above the *Aphelaspis* Zone in the Great Basin of the western United States, Palmer was struck by the similarity of the faunal turnover at the top of the *Elvinia* Zone to that which occurs at the top of the *Crepicephalus* Zone. At both boundaries a taxonomically and morphologically diverse trilobite assemblage is replaced by a high-abundance, low-diversity fauna dominated by olenimorphs. Palmer attributed these replacement faunas to successive invasions of the shelf by a slowly evolving stock of trilobites that inhabited deeper water, off-shelf environments (Palmer 1965b). He posited that the invading deep-water forms annihilated the diverse platform faunas and then "evolved in place" to produce the series of new genera and species that characterise the overlying zones, whose dominant elements he linked through a series of evolutionary lineages. The superzonal unit bracketed by the olenimorph faunas, from the base of the *Aphelaspis* Zone to the top of the *Elvinia* Zone, he named the Pterocephaliid Biomere.

In justifying the introduction of a new type of biostratigraphic unit, Palmer (1965b) noted that these major horizons of faunal turnover did not correspond with any of the boundaries used to divide the Upper Cambrian Series into stages in the standard nearshore clastic succession of the northern midcontinent. Additionally, some biostratigraphic data available at the time led him to suspect that the invading deeper water fauna may have replaced the shallow water forms somewhat earlier in more distal sites on the platform. Thus the term biomere was introduced for a stage-level biostratigraphic unit with potentially diachronous boundaries marked by "...abrupt non-evolutionary changes in the dominant elements of a single phylum". Characterisation of the boundary as 'abrupt' was justified by stratigraphic separation of the extinguished and replacement faunas by only centimetres in some sections. Palmer noted a lack of lithologic evidence of environmental change(s) accompanying the faunal change as another remarkable property of biomere boundaries.

Susan Longacre, a Ph.D. student under the tutelage of Charlie Bell at the University of Texas, described a second biomere on collections from numerous measured sections in the Llano Uplift of central Texas (Longacre 1970). She demonstrated the diversification of trilobites from the base of the *Taenicephalus* Zone up through the top of the *Saukia* Zone and reconstructed phylogenies for several families. After protracted consideration of several families for which the new biomere might be named, she selected the Ptychaspididae and named the interval the Ptychaspid Biomere.

Biomeres Refined (1971-1977)

James H. Stitt (Fig. 2B), a contemporary of Longacre's and also a doctoral student under Charlie Bell, documented a similar faunal succession through the Ptychaspid Biomere in southern Oklahoma (Stitt 1971a). Jim Stitt was an exceptionally methodical and diligent individual whose sampling of the fairly well-exposed, but only sparsely fossiliferous Upper Cambrian strata in the Arbuckle Mountains produced a data set (Stitt 1971a) that has been drawn upon heavily in many subsequent studies (see below). Stitt sampled the entire 500-550 m Upper Cambrian succession, splitting rock from each 0.3 m (1-foot) interval for a minimum of 10 minutes, thereby covering approximately 15 m of section per day.

Comparing his species range data with those from other areas of North America, Stitt (1971b, 1975) recognised four evolutionary stages within the biomere that he related to the components of adaptive radiation described by Simpson (1953) in studying Cenozoic mammals. Stitt described the fauna of stage 1, the initial stage of adaptive radiation at the base of the biomere, as a low diversity assemblage of species that display short stratigraphic ranges, high intraspecific variability, and a relatively limited range of morphology overall. Within stage 2, which he interpreted as the "consolidation phase", some species display longer stratigraphic ranges, intraspecific variability is reduced, and the overall range of morphologies is greater than observed in stage 1. These trends continue into stage 3, wherein long-ranging species with limited intraspecific variability and little if any morphologic intergradation between genera represent a stable shelf community. The top of stage 3 is a subzonal boundary at which an extinction event erased most of the taxonomic diversity and morphologic variation gained during stages 1-3. Above that horizon is stage 4, a thin stratigraphic interval that is dominated by one opportunistic genus or species that survived the extinction to proliferate and form dense shell concentrations (sometimes true coquinas) in shallow platform settings. Stitt (1971b, 1975, 1977) identified the *Irvingella major* Subzone of the *Elvinia* Zone as stage 4 of the Pterocephaliid Biomere and the *Eurekia apopsis* (= *Corbinia apopsis*) Subzone of the *Saukia* Zone as stage 4 of the Ptychaspid Biomere (Fig. 3). The fauna within stage 4 also includes some "exotic" taxa, clearly not related to genera from stage 3, that migrated in from deep water environments (e.g., *Comanchia* in the *I. major* Subzone and *Larifugula* and *Apatokephaloides* in the *E. apopsis* Subzone). Stitt interpreted this stage as representing a time of "evolutionary desperation" during which the platform fauna struggled to cope with the new environmental conditions and compete with the first immigrants from deeper water sites. Stitt's stage 4 is the "critical interval" to which I refer throughout this paper. A revision of the numbering sequence subsequently proposed by Palmer (1979) for the internal stages is discussed below.

Stitt (1975, 1977) also provided a detailed extinction scenario for consideration and testing. As the extinction mechanism, he proposed a rise in the oceanic thermocline, which allowed the cooler waters of the deep ocean to impinge upon the shelf and exterminate the thermophilic platform taxa. Olenid or olenid-derived deep-water forms migrated onto the shelf to repopulate the shallow water environments. Stitt (1975, p. 389) even identified a potential olenid ancestor (*Parabolina*) for *Parabolinoides*, the olenimorph that dominates the basal fauna of the Ptychaspid Biomere. His extinction model, which he cautioned was probably oversimplified, was consistent with the information available at the time that he proposed it.

The mid to late 1970's was an exciting time in palaeontology when the discipline expanded to address issues and incorporate concepts from the biological sciences more rigorously, and often more quantitatively, than had been done in the past. Deductive models that sought to explain evolutionary patterns were popular and Cambrian biomeres offered plenty of grist for the mill. Palaeobiology emerged as an area of active study within the discipline and spawned a new journal for researchers to publish the results of their research on micro- and macroevolution. Ashton & Rowell (1975) evaluated some of Stitt's evolutionary hypotheses in the inaugural volume of Paleobiology, utilising data from the Pterocephaliid Biomere in the Great Basin. They did not dispute that range data from previous studies in different regions demonstrate that species richness and average stratigraphic ranges of species in Stitt's stage 3 were greater than those in stage 1. However, their quantitative analysis did not support his contention that within-species variation is greatest at the base of the biomere and is significantly reduced at stratigraphically higher levels. Eldredge (1977) also commented on Stitt's evolutionary model, cautioning that his interpretations, while 'imaginative', were as yet untested.

Biomeres Revised (1979-1984)

Two factors contributed to an emphasis on high-resolution sampling in biostratigraphic research conducted during this interval of time. International working groups had been established under the auspices of the International Union of Geological

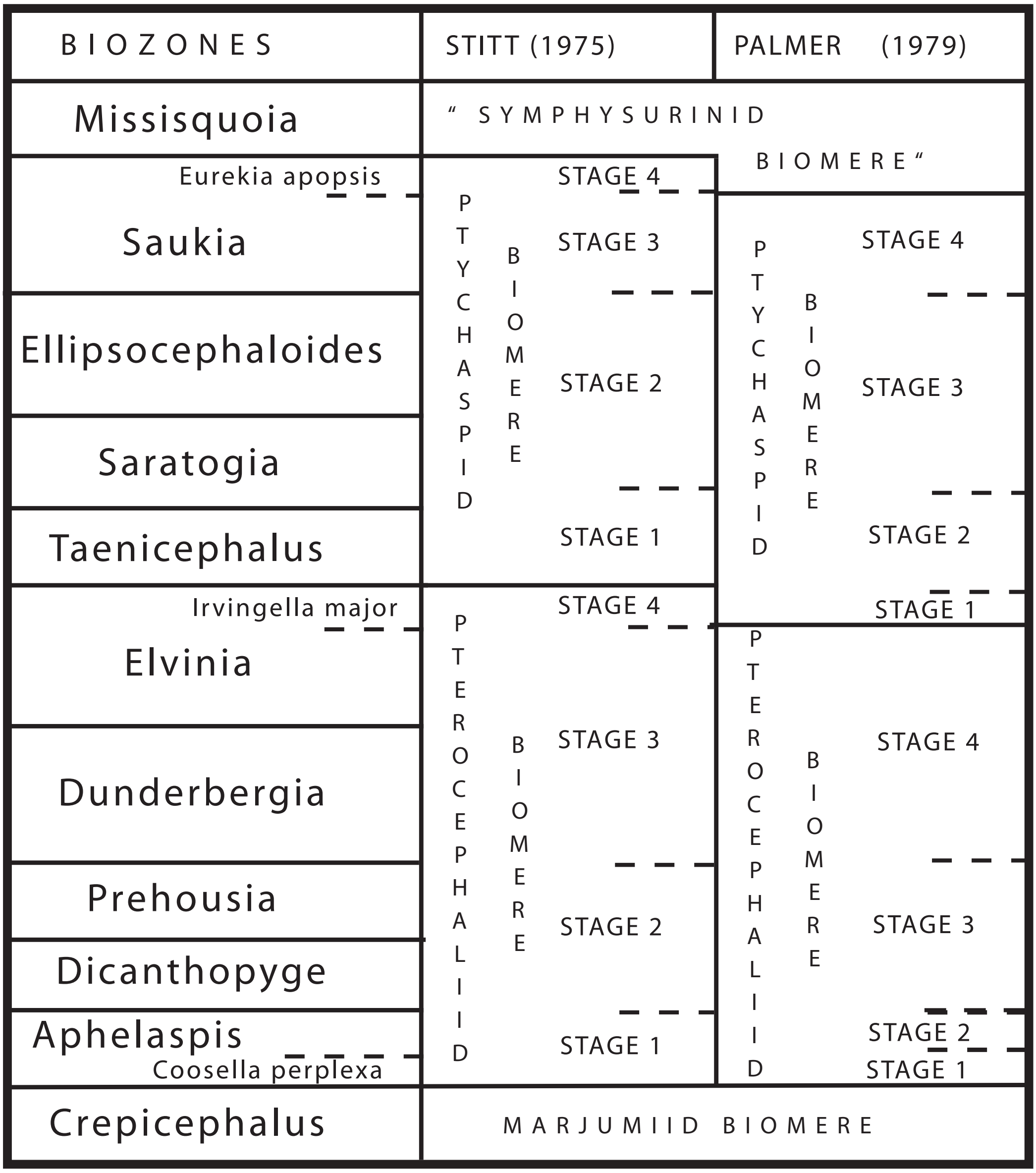

Fig. 3. Developmental 'stages' recognised by Stitt (1971b, 1975) within Upper Cambrian biomeres and revisions proposed by Palmer (1979) in placement of biomere boundaries and numbering of the internal stages (after Palmer 1979). Although Palmer's figure showed the base of the Pterocephaliid Biomere as interpreted by Stitt coinciding with the base of the *Coosella perplexa* Subzone, Stitt actually considered that subzone to be stage 4 of the underlying Marjumiid Biomere.

Sciences to select boundary stratotypes for several system and series boundaries, among them the Cambrian-Ordovician boundary. Established in 1974, the International Working Group on the Cambrian-Ordovician Boundary was well underway with its intensive sampling of the most complete sedimentary successions spanning this system boundary on all continents. By the early 1980s, a number of excellent candidate sections had been identified and sampled (Bassett & Dean, 1982). In North America, suitably thick, highly fossiliferous, and well-exposed successions had been sampled in the western United States (Miller *et al*. 1982), northwestern Canada (Ludvigsen 1982) and Newfoundland (Fortey *et al*. 1982; Fortey 1983). The data provided by sub-metre-scale sampling of highest Cambrian and lowest Ordovician strata throughout North America greatly refined correlations with coeval rocks on other continents and ultimately resulted in selection of a boundary stratotype for the base of the Ordovician System (Cooper *et al*. 2001). It also provided a wealth of new data regarding the vertical and biogeographic patterns of faunal change at the top of the Ptychaspid Biomere.

Additional impetus for high-resolution sampling was provided by publication of the controversial Alvarez Hypothesis (Alvarez *et al*. 1980), which triggered a frenzied search for physical and geochemical evidence of extraterrestrial impact at horizons of faunal turnover throughout the stratigraphic column. Palmer (1982) quickly proposed biomere extinction horizons as plausible candidates for consideration, a proposal justified in part by evidence that they appear to correlate with faunal crises on other palaeocontinents. In Australia, for example, Öpik (1966, 1967) described an 'early Upper Cambrian crisis' at the boundary between the Mindyallan and Idamean Stages, which correlates precisely with the base of the Pterocephaliid Biomere. However, interest quickly waned when geochemical anaylses revealed no evidence of elevated Iridium concentrations or other impact indicators (Orth *et al*. 1984). Additionally, all the high-resolution biostratigraphic data demonstrated that faunal turnover at each biomere boundary was not instantaneous even in a geologic sense. A step-wise decline in diversity through one or more biostratigraphic units spanning several metres of strata clearly was incompatible with an impact scenario (Ludvigsen & Westrop 1983; Palmer 1984).

Intrigued with the thin critical interval (stage 4) discovered by Stitt in Oklahoma, Palmer returned to some of his sections in the Great Basin and conducted intensive, centimetre-scale sampling across the base of the Pterocephaliid Biomere. He discovered that there was indeed a thin interval above the main extinction horizon that was dominated by a taxon clearly related to the fauna of the underlying *Crepicephalus* Zone. He named this interval the *Coosella perplexa* Subzone for the dominant species. However, in the paper reporting his findings (Palmer 1979), he proposed a revision of the biomere concept, repositioning the biomere boundary to correspond with the major extinction horizon at the base, rather than the top of the critical interval. He argued that Stitt's stage 4 should be considered stage 1 of the overlying biomere, as it represents the start of the immigration and replacement process (Fig. 3). Additionally, turnover of other (non-trilobite) faunal groups is more pronounced at the base of the crisis interval, attesting to the significance of that horizon and expediting recognition of the event even on other palaeocontinents.

The proposed revision was not popular with many biomere workers for reasons expressed by Stitt (1983, p. 17) who noted that, with the proposed revision, "..the base of the overlying biomere would be defined by important and abundant elements from the dominant families of the underlying biomere, which would destroy the important concept of the phylogenetic entity of a biomere." As a result, the placement of the biomere boundary became a contentious issue and some practitioners continue (to the present day) to use the original concept of the biomere where the crisis interval constitutes stage 4 of the underlying biomere. Some workers (e.g. Fortey 1989, p. 97) chose to avoid the issue altogether rather than risk becoming mired in that debate.

In contrast, the redefinition was embraced readily by Rolf Ludvigsen (Fig. 4), who described the faunal succession through the Cambrian-Ordovician boundary interval in northwestern Canada (Ludvigsen 1982). Ludvigsen's perspective on biomeres and their bounding extinctions differed from those of previous investigators for several reasons. First, he did not complete a dissertation on Cambrian trilobites under Charlie Bell, but received his Ph.D. from University of Western Ontario, where he described silicified Ordovician trilobites under the supervision of Alf Lenz. Secondly, Ludvigsen's outlook on the biomeres differed because the lithofacies and faunas that he described represented more distal and deeper environments than those in which the biomeres had been described and refined. The taxonomic content and response of these deep shelf to upper slope faunas to the events of the critical interval differ somewhat from that of their shallow water counterparts. In the more distal setting the fauna immediately above the mass extinction horizon (stage 3/stage 4 boundary of Stitt) contains a significantly higher percentage of deep-water immigrants, reinforcing Palmer's contention that the base of the critical interval represents the beginning of the replacement process. Similarly, the pre-extinction fauna contains some of the 'exotic' taxa (e.g. *Larifugula*) that appear for the first time as immigrants within the critical interval in more proximal facies.

The strong contrast in taxonomic content of the fauna within each zone of his study interval with its platform counterparts, a phenomenon with which he was quite familiar from previous work on trilobite biofacies (distinct, environmentally-controlled, and time-averaged trilobite associations) in the Middle Ordovician (Ludvigsen 1979), led Ludvigsen to argue that previous studies on biomeres had overemphasised

Fig. 4. Rolf Ludvigsen (left, with wine glass), trilobite specialist at University of Toronto in the 1980's and first to challenge the interpretation of biomeres as entirely the products of *in situ* speciation on the Laurentian platform. Photo provided by Ludvigsen who, as editor of *Palaeontographica Canadiana*, was showing the inaugural issue of this monographic series to Geoff Norris, Chair of the Geology Department, in November, 1983.

Fig. 5. Richard A. Fortey of the Natural History Museum in London, UK, among the first to recognise the importance of shoreward migration of shelfbreak and off-platform taxa in the diversification process and also to challenge the family-level uniqueness of faunas in successive biomeres. Photo provided by Fortey, taken in 2002.

the vertical patterns of faunal turnover in isolated measured sections and failed to consider lateral variations in the make-up of platform faunas. He suggested that lateral migration of biofacies might have contributed significantly to the faunal changes within biomeres that had been attributed entirely to evolutionary processes. Ludvigsen (1982) was among the first to challenge the premise that diversification up-section through the biomere is entirely the result of *in situ* speciation from the invading oceanic stock, citing as one cause for scepticism the extreme evolutionary rates calculated by Stanley (1979) for trilobites of the Ptychaspid Biomere based on that premise. He pointed out that species within stage 3 of the two best-documented biomeres were assigned to 8 (Pterocephaliid Biomere) and 11 (Ptychaspid Biomere) families and argued, therefore, that an estimate of about 10 ancestral species would be more reasonable than the 5 species estimated by Stanley and would bring the calculated speciation rates in line with those seen in other groups. Richard Fortey (Fig. 5) of the Natural History Museum in London, UK, arrived independently at similar conclusions based on his work on shelfbreak faunas in uppermost Cambrian and basal Ordovician toe-of-slope limestone conglomerates in Newfoundland. Like Ludvigsen, Fortey (1983) concluded that immigration of taxa from outer shelf and upper slope environments contributed significantly to the diversification of platform trilobite faunas through the biomere.

Ludvigsen (1982) also questioned the prevailing view that biomere boundaries are not marked by lithofacies change, noting the approximate coincidence of the biomere extinction horizon with a change from platform lithofacies to slope deposits (i.e., a Grand Cycle boundary *sensu* Aitkin 1966) in his sections in Canada. Earlier studies (Cook & Taylor 1975; Taylor 1977) had documented that the Cambrian shelfbreak constituted not only a major sedimentological boundary, but also the transition from one palaeobiogeographic province to another. Noting this correspondence, Ludvigsen (1982) argued that biogeographic models held more promise than evolutionary models for an explanation of the faunal turnover. In particular, he suggested that sea level rise caused a shoreward shift of the province boundary, triggering extinctions through reorganisation of shelf biofacies and

STAGE	ZONE	Mackenzie Mountains (Ludvigsen, 1982)		Alberta (Westrop, 1986)		Oklahoma (Stitt, 1971, 1977)	INTERVAL (Westrop, 1989)	
Ibexian	Parabolinella	Apoplanias rejectus	Missisquoia	Missisquoia typicalis	Missisquoia	Missisquoia typicalis	Typicalis	"SYM. BIO."
		Missisquoia depressa		Missisquoia depressa		Missisquoia depressa	Depressa	PTYCHASPID BIOMERE
		Missisquoia mackenziensis		Not recognized		Not recognized		
	Yukonaspis	Elkanaspis corrugata	Saukia	Eurekia apopsis	Saukia	Eurekia apopsis	Apopsis	
Sunwaptan		Bowmania americana		Stenopilus glaber		Saukiella serotina	Serotina	

Fig. 6. Environmentally controlled variation of zonal and subzonal nomenclature through the Ptychaspid-Symphysurinid Biomere boundary. Placement of the biomere boundary at the base of the "*typicalis* Interval", which is higher than in previous studies, is justified by the appearance of a fauna dominated by the olenid trilobite *Apoplanias* at the base of that interval throughout North America (Taylor 1997; Myrow *et al*. 1999). Strong biofacies differentiation apparent in the pre-extinction *serotina* Interval is the result of distinct faunas linked to deep shelf/upper slope (*B. americana*), platform microbial reef (*S. glaber*), and level-bottom subtidal carbonate (*S. serotina*) lithofacies. After Westrop & Cuggy (1999).

diminished shallow shelf area. Ludvigsen and his Ph.D. student Stephen Westrop, whose dissertation focused on rich Upper Cambrian and Lower Ordovician trilobite faunas in Alberta, subsequently provided an expanded treatment (Ludvigsen & Westrop 1983) on trilobite biofacies of the Cambrian-Ordovician boundary interval in North America. In that paper they restated their preferences for a biogeographic extinction mechanism and promised that a fuller critique of the biomere concept would be provided elsewhere. They delivered on that promise in a series of papers in the latter half of the decade.

Biomeres Reviled (1985-1990)

Ludvigsen & Westrop (1985) proposed a revised stadial nomenclature for the Upper Cambrian of Laurentia that replaced the traditional Dresbachian, Franconian, and Trempealeauan Stages from the Upper Mississippi Valley region with new stages that corresponded with the three biomeres (Fig. 6), utilising the revised boundaries proposed by Palmer (1979). Additionally, they argued that adoption of these intervals as stages rendered the biomere redundant and recommended that use of the term be discontinued. Although a significant number of Lower Palaeozoic specialists promptly responded with strong criticism to this proposal (Robison *et al*. 1985), different individuals for different reasons, the new stages have proven useful and are incorporated in the most recent chronostratigraphic scheme proposed for Laurentian North America (Palmer 1998). Biomeres, however, have not passed quietly into history.

Another challenge to the biomere concept, or at least to the contention that Stitt's stages 1-3 represent a true adaptive radiation, came from a statistical analysis of species diversity data through the Ptychaspid Biomere in Oklahoma by Margaret Hardy. Utilising Jim Stitt's published data from the Arbuckle (Stitt 1971a) and Wichita (Stitt 1977) Mountains, Hardy (1985) concluded that the observed diversity patterns were more likely the product of biofacies migrations rather than *in situ* adaptive radiation. In her acknowledgements, Hardy expressed her appreciation foremost to Jim Stitt, who provided her not only with the data set on which her paper was based, but also with extensive and patient guidance and constructive criticism in her study. That will come of no surprise to anyone who had the privilege of knowing and working with Jim Stitt prior to his untimely death in September 1999 at the relatively young age of 69. He was an extraordinary gentleman and a valued colleague to many in the international community of trilobitologists and Lower Palaeozoic specialists (Taylor 2000). However, he did live long enough to see the results of Hardy's study contradicted by a more extensive analysis of Upper Cambrian trilobite diversity (Westrop 1988) that considered diversity increases documented in sections throughout North America. Westrop rejected Hardy's conclusions as an artifact of a geographically restricted data set and recognised a significant role for endemic speciation on the shelf for the diversification of Laurentian trilobite faunas through the Sunwaptan Stage (Ptychaspid Biomere). However, Westrop's study also required some revision of Stitt's evolutionary model. Although his analysis confirmed a continuous diversification of Laurentian faunas as a whole through stages 1-3, separate analysis of subtidal platform faunas versus shelf margin faunas revealed that only the latter display significant diversity increases through the upper half of the stage.

Westrop & Ludvigsen published extensively (Westrop & Ludvigsen 1987; Westrop 1988, 1989, 1990) through the end of the decade on the patterns of diversification through the latest Cambrian and also the faunal replacement across the Cambrian-Ordovician Boundary (i.e, across the top of the Ptychaspid Biomere), assiduously using the term 'biomere' always in quotations and for historical reference. Utilising a greatly expanded database that included considerable new stratigraphic range data for species in outer shelf to slope facies, they provided rigorous statistical evaluation of survivorship through a 'critical period' comprising the *Eurekia apopsis* and *Missisquoia depressa* Subzones and their correlates, referred to for simplicity as the *apopsis* and *depressa* Intervals (Fig. 6). Data from the underlying pre-extinction *serotina* Interval (*Saukiella serotina* Subzone) and overlying post-extinction *typicalis* Interval (*Missisquoia typicalis* Subzone) were included in the analysis for comparison. This is the interval through which taxa of the Ptychaspid Biomere are ultimately replaced by those of the Symphysurinid Biomere (formerly referred to informally as the "hystricurid" biomere by Stitt [1977] and Ludvigsen [1982], but renamed by Stitt [1983]).

In the first of these papers, Westrop & Ludvigsen (1987) focused on extinction mechanisms, criticising those proposed in previous studies and offering as an alternative the effects of biogeographic reorganisation in response to sea level rise. They rejected outright an incursion of cold and/or poorly oxygenated waters from the ocean basin with a rise of the oceanic thermocline, the mechanism favored by Palmer (1965a, 1984) and Stitt (1971a, 1975, 1977), citing the absence of physical evidence of environmental change at biomere boundaries. They interpreted the continued deposition of shallow carbonate platform lithofacies and the absence of dark, pyritic lithologies in the boundary interval as conclusive evidence that no significant drop in water temperature or oxygenation (respectively) had accompanied the faunal turnover. In contrast, they reported that faunal changes through the extinction interval involve a progressive up-section increase in percentage of shelf margin or off-shelf taxa and a concomitant reduction in the number of differentiated biofacies in shelf environments from four (immediately prior to the onset of extinctions) to one by the end of the replacement process. Their model attributed the high extinction rates through the crisis period to elimination and merging of platform biofacies caused by shoreward displacement of distal platform environments and faunas.

Westrop (1989, 1990) also criticised the temperature/oxygen decline scenario on theoretical grounds because it invokes upward causation *sensu* Vrba & Gould (1986) in assuming that the extinction of higher-level taxa (genera and families) during the critical period resulted from collective failure of constituent species to cope with changes in specific environmental parameters. He argued that this was a testable hypothesis inasmuch as upward causation should be expressed in greater average species longevity (longer stratigraphic ranges) for species representing families that survived the extinction interval as compared to those that belong to families that did not survive. The range data for species occurring in the critical interval revealed no such contrast. Additionally, his analysis revealed a considerably higher survival rate for pandemic versus endemic families in the critical interval. He concluded, on the grounds that geographic distribution is a property emergent above the individual organism level, that sorting of clades during the extinction was not the product of upward causation.

However, Westrop's conclusions can be challenged on conceptual and procedural grounds. Conceptually, there is some question as to whether a species' propensity to survive should be viewed as a character emergent at the species level. It would be more consistent with the concept to view extinction resistance as simply a character of individual organisms that make up the species (Eldredge 1989; Lieberman & Vrba 1995). Regardless of its conceptual foundation, Westrop's analysis suffers from a critical procedural flaw in that it included only those species that occur in the *apopsis* Interval or higher subzones; it specifically excluded the large number of species of the highly diverse *serotina* Interval whose ranges terminate upward at the extinction horizon marking the top of the Sunwaptan Stage. Therefore, his study evaluates only the properties and fates of a greatly reduced subset of the diverse shelf fauna, which already had been selected for their potential for survival, and the immigrant taxa that arrived following the first major extinction event. One must then question the confident dismissal of temperature and/or oxygen decline (and thus upward causation) as the cause of mortality in the initial phase of extinction and replacement. Contrary to Westrop's assertion, others have continued to include temperature and oxygen crises in discussing the possible causes of extinctions across the Cambrian-Ordovician boundary. Fortey (1989), for example, considered movement of poorly-oxygenated waters onto the shelf as the most plausible mechanism for explaining the migration of olenimorphs into shallow marine settings in the latest Cambrian and early Ordovician.

On the other hand, Fortey had his own reservations about the biomere concept. First (Fortey 1989), he expressed concern that potentially incomplete or incorrect reconstruction of phylogenetic relationships within and between biomeres has resulted in overestimation of the magnitude of boundary extinctions, particularly those documented across the Cambrian-Ordovician boundary (i.e., the top of the Ptychaspid Biomere). The crux of the problem is the difficulty in linking early plesiomorphic (primitive) groups that occur immediately above levels of extinction, and directly below intervals of rapid divergence (cladogenesis), with more derived descendants and relatives. In the absence of reliable characters to establish such linkages, many groups have been set apart in their own paraphyletic genera or families whose highest stratigraphic occurrences are then misinterpreted as true extinctions of superspecific groups. Such "taxonomic pseudoextinctions" (Briggs *et al*. 1988; Fortey 1989), for example, where other taxa succeed the olenimorphs just above the base of each biomere, will clearly impede accurate assessment of relationships of related taxa within and between biomeres.

Note the arrival at this point of the influence of another revolution in the palaeontological community - the emergence of phylogenetic systematics (Hennig 1966; Wiley 1981) or 'cladistics' as the methodology of choice for reconstruction of phylogenies. A movement to revaluate relationships among trilobite taxa utilising this powerful method was underway by the end of the 1970s (Eldredge 1979; Eldredge & Branisa 1980), and it was not long until it was utilised in the study of lower Palaeozoic trilobites (e.g., Fortey & Chatterton 1988). In this context, Fortey & Owens (1990) questioned the taxonomic basis of the biomere concept, specifically the continued interpretation of the majority of taxa as North American endemics derived by *in situ* speciation on the Laurentian shelf. Although they (Fortey & Owens 1990, p. 155) conceded that "There is no doubt of the reality of the biomere as a stratigraphic pattern in the distribution of species..." they asserted that Cambrian trilobite families had been defined with too little morphologic analysis and perhaps too much consideration of stratigraphic position. They went so far as to offer that "...a sceptic might wonder whether the biomere concept controls the taxonomy to the extent that it becomes self fulfilling." Additionally, Fortey & Owens cautioned that the interpretation of many taxa as endemic to Laurentian North America might reflect the far less complete documentation of coeval faunas on other continents.

It was not long before their hypothesis was put to the test. Edgecombe (1992) provided a cladistic reappraisal of families in the Ptychaspid Biomere, excluding any consideration of stratigraphic position of the taxa involved, and concluded that "biomere phylogeneticists" had indeed been too strongly influenced by spatiotemporal data. Extending the stratigraphic ranges of Ptychaspid Biomere families to account for recent revisions of some families entirely on morphologic grounds (Ludvigsen & Westrop 1983; Westrop 1986; Ludvigsen *et al*. 1989), as well as the addition of "ghost lineages" (Norell 1992) dictated by the lowest documented occurrences of sister taxa, Edgecombe argued that the concept of a biomere as an extinction-bounded closed system was largely an artifact of pseudoextinctions of non-monophyletic groups.

Biomeres Revived (1993-1999)

Most papers on biomeres in the early 1990s dealt primarily with the debate regarding the cause(s) of extinctions across their boundaries. Loch *et al*. (1993) described the faunal succession across the Cambrian-Ordovician boundary at Mount Wilson, Alberta, utilising collections made by James R. Derby and Brian S. Norford in 1970. These collections allowed more precise placement of the zonal and subzonal boundaries than was possible in earlier studies that incorporated data from Mount Wilson (Dean 1978, 1989; Westrop 1986). They confirmed that the extinction horizon at the top of the Sunwaptan Stage (base of the *apopsis* Interval) does not coincide with the change from limestone to shale that marks a Grand Cycle boundary (the base of the Survey Peak Formation), as was claimed in previous studies (Westrop 1986, 1989; Westrop & Ludvigsen 1987) that invoked an abrupt shoreward shift of lithofacies and biofacies as the cause of the extinctions. At Mount Wilson the extinction horizon actually lies more than 20 m above the Grand Cycle boundary. Utilising Graphic Correlation, Loch *et al*. (1993, fig. 5) also demonstrated that the onset of shale deposition occurred somewhat later at Wilcox Peak, approximately 20 km northwest of Mount Wilson. Given the diachronous nature of the replacement of limestone with shale deposition, the significant stratigraphic separation of the extinction horizon from the Grand Cycle boundary, and a lack of evidence of transgression in the boundary interval in the Great Basin (Taylor & Cook 1976), Texas (Winston & Nicholls 1967) and Oklahoma (Stitt 1971a, 1977), Loch *et al*. (1993) rejected the Westrop and Ludvigsen onlap hypothesis, suggesting that an advancing wedge of cold/anoxic water remained the mechanism most consistent with the available data from all areas. Subsequent detailed biostratigraphic studies across the top of the Ptychaspid Biomere in inner shelf clastics in New Mexico (Taylor & Repetski 1995) and the base of the Ptychaspid Biomere in proximal carbonate platform facies in Pennsylvania (Loch & Taylor 1995; Taylor *et al*. 1999) also revealed no evidence of deepening or onshore migration of facies that coincided precisely with either the stage boundaries or the biomere boundaries. Thus again the validity of the onlap hypothesis must be questioned.

All investigators have been hampered by the ambiguity of the physical evidence and perhaps the interdependence of the environmental parameters. Onlap of lithofacies, particularly in outer shelf locations, may result from a rise in sea level or, as suggested by Loch *et al*. (1993, p. 505), from decreased rates of carbonate sediment generation caused by a drop in water temperature. For example, lithologic evidence at base of the Ptychaspid Biomere in Wyoming prompted Matthew Saltzman (Saltzman *et al*. 1995; Saltzman 1999) to propose a role for both sea level rise and a reduction in water temperature and oxygen content. In that area, the extinctions were accompanied by destruction of the non-skeletal carbonate factory comprising oolitic shoals and thrombolitic reefs. The thin, coquinoid concentrations of trilobites and brachiopods in the overlying *Irvingella major* and *Parabolinoides* Subzones invite comparison with cool water carbonates that accumulated on high latitude shelf areas throughout the late Cambrian. Taylor *et al*. (1999) also reported the disappearance of thrombolitic reefs at the Pterocephaliid-Ptychaspid Biomere boundary in the Appalachians, but found no physical evidence of deepening across the biomere boundary to suggest that the reefs had been "drowned", as interpreted by Saltzman for the Wyoming succession.

Some studies in the 1990s employed isotopic analysis in the hope that geochemical data would confirm or disprove the involvement of temperature and/or oxygen changes. Saltzman *et al*. (1995) and Saltzman (1999) documented trends toward lower $^{87}Sr/^{86}Sr$ ratios and more positive $\delta^{13}C$ values upward across the base of the Ptychaspid Biomere. They interpreted the change in strontium isotope ratios as the consequence of progressive sea level rise and the positive trend in carbon isotopes as evidence that the extinctions were caused by reduced oxygen concentrations. In an integrated sedimentological and geochemical study of Upper Cambrian strata in the Great Basin and Appalachians, Montanez *et al*. (1996) documented similar concurrent trends in carbon and strontium isotopes, linking them to sea level rise during deposition of the highest part of the Marjumiid Biomere and basal strata of the Pterocephaliid Biomere. In a very detailed study that involved sub-metre-scale sampling of the same stratigraphic interval in the Black Hills of South Dakota, Perfetta *et al*. (1999) discovered a small but abrupt negative shift in $\delta^{13}C$ values, superimposed on the general positive trend, precisely at the base of the *Aphelaspis* Zone (=base of Pterocephaliid Biomere). They noted a similar shift apparent in the curves provided by Saltzman *et al*. (1995) for the base of the Ptychaspid Biomere and posited that the similarity reflects a common mechanism for all biomere boundary extinctions. The model proposed by Perfetta *et al*. (1999) acknowledges onlap, initiated well in advance of the extinctions, as setting the stage for the faunal turnover, but attributes the demise of the platform fauna to an incursion of cool ^{12}C-enriched waters from the deep ocean as a result of either a rise in the oceanic thermocline or destratification of the ocean coincident with the biomere boundary. They also noted a shoreward decrease in the magnitude of the negative excursion and suggested that this might reflect a stronger influence for the cold waters where they first impinged on the palaeoshelf. Similarly detailed and integrated analysis of the patterns of isotope and lithofacies change across the top of the Ptychaspid Biomere in shallow shelf facies in Wyoming and Montana to test this hypothesis is currently in progress (Ripperdan *et al*. 2000; Ripperdan 2002). Although the geochemical data reported from biomere boundary intervals are consistent with an influx of cold and/or oxygen-poor waters, they should not be viewed as confirming that scenario. When the number of factors that can bring about a change in the isotopic composition of sea water are considered (see Ripperdan 2001), it is clear that alternative explanations to temperature and/or oxygen decline can be devised.

The latter half of the 1990s saw a resurgence of discussion regarding the definition and significance of biomeres as macorevolutionary units. Westrop (1996, p. 43) opined that "'Biomeres' are parochial North American units and their usage should be discontinued." Conversely, I argued (Taylor 1997, Myrow *et al*. 1999) that the palaeogeographic restriction of the biomere phenomenon to the Laurentian shelf is hardly cause for abandonment of remarkable, natural units of evolutionary significance in the Upper Cambrian of that palaeocontinent. However, the biomeres that I defended were those whose boundaries conform to the levels used prior to Palmer's (1979) revision, with one very important exception, the top of the Ptychaspid Biomere, which I placed at the base of the *typicalis* interval (*Missisquoia typicalis* Subzone) (Fig. 3), two subzones higher than Palmer (1979) and one subzone higher than Stitt (1971b, 1975, 1983).

In preparing presentations for the 2nd International Trilobite Conference in August 1997, I chose the biomere concept as a topic of one talk to invite criticism of the views I'd held for many years, some of them the products of years of tutelage under Jim Stitt at the University of Missouri. My primary goal was to establish whether my opinion that biomeres are not merely stages but something different was well-founded in data and sound analysis. The first step in the process was a review of the pertinent literature and relevant biostratigraphic data, including my own from nearly two decades of systematic study of biomere boundaries. The crucial issues were: 1) the criteria for defining biomere boundaries and 2) whether those criteria identified horizons other than the stage boundaries.

Stitt (1983) had rejected Palmer's (1979) redefinition of the biomere, arguing that it would break the phylogenetic continuity of the biomere by assigning the highest subzone (his stage 4) dominated by a species representing one of the major families of the underlying biomere to the base of the overyling biomere. Yet his own selection for the top of the Ptychaspid Biomere, the base of the *Missisquoia depressa* Subzone, did exactly that. The *M. depressa* Subzone is dominated in most platform sections by one or more species of *Plethopeltis*, which represents one of the dominant families (Plethopeltidae) of the Ptychaspid Biomere. The other inconsistency that had always troubled me in Stitt's model was his assertion that *Plethopeltis arbucklensis* was the generalised, highly variable opportunist that marked the base (stage 1) of the Symphysurinid Biomere, equating it in that regard with *Aphelaspis* and *Parabolinoides* at the bases of the Pterocephaliid and Ptychaspid Biomeres, respectively. Although it is true that *P. arbuckelensis* dominates the fauna to the same degree and displays appreciable intraspecific variability, it is a rather derived, effaced form rather than a generalised olenimorph comparable to those whose appearances define lower biomere boundaries.

Confronted with these inconsistencies in the definition of the biomere bounaries, I came close to concluding that the concept had outlived its usefulness. But then it occurred to me that perhaps stage 4 of the Ptychaspid Biomere comprised more than a single subzone, and the true base of the overlying Symphysurinid Biomere lay at a higher level. Following that logic, I looked to the next higher subzonal boundary, the base of the *Missisquoia typicalis* Subzone, and realised that we had indeed overlooked the true analog of the *Aphelaspis* and *Parabolinoides* faunas. What wasn't known at the time Stitt (1975, 1977) delineated the internal stages of the Ptychaspid Biomere was that the base of the *M. typicalis* Subzone in most sections is not marked by the appearance of that species but by the prolific and usually monotaxic occurrence of the olenid trilobite *Apoplanias rejectus*. This "*Apoplanias* Fauna" was discovered through precise sampling in a number of subsequent studies (Ludvigsen 1982; Taylor 1984; Loch *et al*. 1993; Taylor & Repetski 1995). What makes the parallel with other biomere boundaries even more striking is the concurrent appearance of dense concentrations of the orthid brachiopod *Apheoorthis*, which can be used, sometimes better than the trilobites, to track the base of the *M. typicalis* Subzone in the same way that coquinas of the strikingly similiar brachiopod *Eoorthis* characterise the base of the *Parabolinoides* Subzone at the base of the Ptychaspid Biomere.

Therefore, the conclusions of my presentation at the 1997 trilobite conference were that: (1) biomeres are not stages; they are different but equally valid superzonal units in the Upper Cambrian of Laurentian North America and (2) each of the three Upper Cambrian biomere boundaries is marked by the appearance of a low-diversity, olenimorph-dominated fauna immediately above the highest occurrence of the dominant families of the underlying biomere. The response was mixed, and anyone who attended the symposium is likely to recall the energetic exchange between Steve Westrop and me in the question/answer session. Foremost among Westrop's objections was that my claim that the biomere boundary marked the highest occurrence of the families of the underlying biomere could be refuted by a number of genera that have been shown to reappear as 'Lazarus Taxa' at some level within the overlying biomere after suffering apparent extinction at the top of the underlying biomere. This objection is valid. As mentioned above, many Cambrian trilobite families are undergoing substantial revision and the resultant extensions of their stratigraphic ranges render the view of biomeres as intervals whose dominant families display no overlap obsolete. However, the validity or reality of the biomere as a stratigraphic unit distinct from a stage does not hinge entirely on whether such overlap exists.

In fact, the relative contribution of immigrants that survived in marginal, non-preserved sites to the overall diversification confirmed (Westrop 1988) through Stitt's stages 1-3 remains one of the most interesting and significant questions yet to be answered by cladistic reappraisal of superspecific relationships in Upper Cambrian and Lower Ordovician trilobites. In other words, to what extent do biomeres 'leak' and to what extent (if at all) did *in situ* speciation and true extinctions through the critical period restrict specific genera to each biomere? Or, in the words of Fortey (2001) in a recent review of accomplishments and remaining challenges in trilobite systematics, "Are 'biomeres' evolutionary packages?"

The placement of the biomere boundaries is obviously a crucial consideration in the pursuit of answers to those questions. Use of Palmer's (1979) revised boundaries, which assigns the critical period (Stitt's stage 4) to the base of the overlying biomere, results in considerable carryover of genera from the faunas below. The biomere thus defined is simply "...a stage, nothing more, nothing less", (Ludvigsen & Westrop 1984), and does not provide a suitable framework within which to compare the relative contributions of immigration and endemic speciation, or otherwise evaluate the evolutionary significance of the biomere. Conversely, the horizon corresponding to the top of the critical interval, where the olenimorph-dominated fauna marks a return to minimum taxonomic diversity, provides a logical point from which to begin monitoring the upward increase in taxonomic and morphologic diversity, the arrival of immigrant taxa from peripheral sites, and *in situ* evolution of some taxa.

BIOMERES IN THE NEW MILLENIUM

It now seems clear from recent improvements in family-level taxonomy of Upper Cambrian trilobites that the phylogenetic uniqueness of each biomere and the magnitude of the boundary extinctions, as measured in true extinction of supergeneric taxa, were overestimated. Many families apparently survived the boundary extinctions and are represented by genera in more than one biomere. Even at the genus level some 'Lazarus Taxa' experience apparent extinction only to reappear later as significant elements of the fauna in the overlying biomere. Thus the earlier view of the biomere as a phylogenetically unique and coherent unit produced by *in situ* speciation in an effectively closed system on the shelf no longer appears defensible. However, the validity of the biomere as a natural unit does not depend entirely on that issue.

Within the shallow marine successions of Laurentian North America, olenimorph-dominated faunas mark three times in the Late Cambrian when the diversity of platform trilobites reached a minimum, each time the result of a series of extinctions that began at a stadial boundary one or two subzones lower. Data reported by Westrop & Cuggy (1999), in a thorough analysis of taxonomic diversity trends through the three biomere boundary extinction intervals, confirm that species richness (alpha or within-habitat diversity) and biofacies differentiation (beta or between-habitat diversity) reached minimum values in the *Aphelaspis* Zone, above the top of the *Coosella perplexa* Subzone (=base of the Pterocephaliid Biomere) and at the base of the *Taenicephalus* Zone (=base of the Ptychapsid Biomere).

Although their data suggest that diversity at the top of the Ptychaspid Biomere dropped to its lowest level in the *Missisquoia depressa* Subzone, I contend that the diversity of the overlying *M. typicalis* Subzone is higher only because taxa that appear above the basal *Apoplanias* Fauna are included in the diversity value reported for that subzone. In sections throughout North America where high-resolution sampling has verified that all the subzones in the critical interval are present, and the position of the base of the *M. typicalis* Subzone (=base of the "Symphysurinid Biomere") has been constrained to less than a metre, *Apoplanias rejectus* is the only species present at the base of that interval (Taylor 1984; Taylor & Repetski 1995; J.F. Taylor unpublished data from Wyoming, Montana, Texas and Minnesota). Therefore, the true diversity minimum in the Ptychaspid-Symphysurinid Biomere boundary interval is represented by an olenimorph-dominated fauna immediately above the top of the critical interval, as is the case at lower biomere boundaries. This is particularly true if morphologic diversity is considered

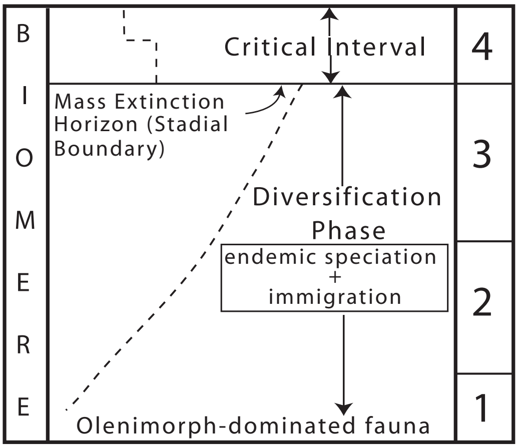

Fig. 7. Revised model of the biomere as a stage-level biostratigraphic package bounded by horizons marked by appearance of minimum-diversity, olenimorph-dominated replacement faunas. In this model, each biomere comprises a diversification phase (Stitt's stages 1-3 - right column) coupled with the overlying critical interval (stage 4) dominated by a surviving genus from the pre-extinction fauna. The dashed line depicts the rise in taxonomic and morphologic diversity of the shallow marine fauna as a whole through both endemic speciation and recruitment of immigrants from distal/off-platform environments. Stepwise decline of diversity shown by dashed line in critical interval is based on patterns documented through *apopsis* and *depressa* Intervals at the top of the Ptychaspid Biomere.

in addition to taxonomic diversity. Although morphologic diversity has been quantified adequately only for the diversification phase of the Marjumiid Biomere (Sundberg 1996), the conservative form of the olenimorphs at each biomere boundary contrasts markedly with the more varied morphologies represented by holdover taxa and immigrants within the underlying critical interval.

Many of us find the natural units between the occurrences of these minimum-diversity, olenimorph-dominated faunas intriguing and useful in studying the repetititve diversification and extinction of faunas on the Laurentian shelf through the Late Cambrian. In my opinion, that is reason enough to retain the biomere as a separate and valid biostratigraphic unit within the shallow shelf deposits of that palaeocontinent. Biomere boundaries become blurred to some degree in deep shelf to upper slope facies (Ludvigsen 1982; Westrop 1995) and perhaps unrecognisable in deeper slope to basinal deposits where the pre-extinction fauna contains numerous olenimorphs and other deep-water groups (e.g., agnostoids) and few shallow-water taxa (Pratt 1992). So they are, indeed, "parochial" (Westrop 1986). However, their restriction to the Laurentian shelf does not compromise their utility in that palaeogeographic context and certainly does not warrant the abandonment of the unit. They are similar to Grand Cycles in that respect, owing their existence to the unique conditions of the Laurentian platform and providing an informative record of the long-term rhythms of environmental change in that setting. Despite all our progress in reconstructing that part of the Cambrian world, many fundamental questions remain unanswered.

Despite the considerable attention given the boundary extinctions, the mechanism(s) responsible for the faunal turnover remain elusive. Additional work is needed to disentangle the effects of sea level change, temperature and oxygen decline, and competition between endemics and immigrants in the critical interval. This may be possible by clever utilisation of data already available, or it may require additional data or new techniques. Whatever the approach, future studies need to address all the extinctions - those at the top of stage 3 and those accomplished through the overlying crisis interval. From the discussion provided in Loch *et al*. (1993, p. 505) on the thickness of the stratigraphic interval through which the boundary extinctions occurred, it is clear that their focus was on species that disappeared at the base of the *apopsis* Interval (=top of Sunwaptan Stage), whereas the turnover quantified by Westrop (1989) dealt with the taxa that occurred within the overlying *apopsis* and *depressa* intervals, and did not address the taxa whose ranges terminated at the stage boundary.

Regardless of whether the biomere is shown through subsequent systematic and biostratigraphic study to be a phylogenetic/evolutionary unit, it is a natural package that represents a 'chapter' in the history of diversity within the platform faunas (Fig. 7). With refinement of correlation of intervals within the diversification phase (stages 1-3) through additional high-resolution biostratigraphic sampling and employment of non-palaeontological chronocorrelation methods, it should be possible to establish more clearly the relative contributions of *in situ* speciation and immigration. Did the latter occur fairly continuously, or can discrete episodes of shoreward dispersion of taxa from distal sites be identified? If immigration occurred at certain times, do associated lithologic and geochemical signals resemble those seen in the boundary intervals to suggest that the boundary perturbations differ only in degree from events that occurred on a more frequent basis? And what of the 'Symphysurinid Biomere'? Will precise biostratigraphic, geochemical, and sedimentological data through the top of the *Paraplethopeltis* Zone closely resemble those from Cambrian biomere boundaries, justifying the biomere label? The biomere has served for more than 40 years as either the focus or the framework for Upper Cambrian trilobite studies in North America. With appropriate vigilance to ensure that the framework does not constrain or unduly influence taxonomic assignments, there is no reason why that service should not continue well into the future.

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