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PALEOBIOGEOGRAPHY AND EVOLUTIONARY RESPONSE DYNAMIC IN THE CRETACEOUS WESTERN INTERIOR SEAWAY OF NORTH AMERICA

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ABSTRACT

Comparison of modern biogeographic divisions with Phanerozoic counterparts reveals numerous methodological and conceptual discrepancies that impair the study of the dynamics and evolution of paleobiogeographic units. By applying modern analytical criteria to the definition of global Cretaceous, mollusc-based, biogeographic divisions, a predictable distribution of these large-scale ecological units is obtained. Cretaceous units were fewer, broader, and had more diffuse ecotonal boundaries than modern analogs. Evidence for Cold Temperate Cretaceous divisions and polar glaciation is lacking. Cretaceous paleobiogeographic divisions reflect broad climatic gradients in a generally warm and equable world. Three paleobiogeographic divisions characterized the Cretaceous Western Interior Seaway of North America during most of its history: a Cool Temperate Northern Interior Subprovince; a Mild Temperate Central Interior Subprovince; and a Warm Temperate Southern Interior Subprovince. To the south lay the Subtropical Gulf and Atlantic Coast Subprovince, and the Tropical Caribbean Province. Stratigraphic data reveal five third-order eustatic cycles which inundated the interior of North America during the Cretaceous. In each, the distribution of paleobiogeographic units was dramatically altered within a 1 to 2 Ma interval around peak transgression and eustatic highstand. These peaks were associated with abrupt paleoceanographic changes involving warming and amelioration of climates, normalization of salinity, and rapid fluctuations between well oxygenated waters and anoxic events. During these 1 to 2 Ma intervals, abrupt northward migration of Subtropical organisms as much as 1500 miles into west-central Canada, and of Tropical reef biotas into the southern United States, depict rapid northward incursions of Subtropical and Warm Temperate biogeographic units. These were followed rapidly by southward emigration to normal distributions. Major extinction events are commonly associated with these incursions, as are periods of rapid evolution among marine taxa. The major centers of endemism and the most rapid rates of evolution in North American Cretaceous molluscs occurred within paleobiogeographic ecotones.

RÉSUMÉ

La comparison des divisions biogéographiques modernes avec des contreparties Phanérozoique révèle de nombreuses méthodologies et conceptualisations inconstantes qui nuisent à l'étude de la dynamique et l'évolution des unités paléobiogeographiques. En applicant des critères analytiques modernes pour définir des divisions biogéographiques du Crétacé globale basé sur des mollusques; on obtient une distribution prévisible de ces unités écologiques de grande échele. Les unités du Crétacé sont moins nombreuses, plus larges et comprennent des limites d'écotone plus diffuses que des analogues modernes. Rien indique une glaciation polaire et des divisions d'un Crétacé Froid. Les divisions paléobiogéographiques du Crétacé réflètent des gradients climatiques larges dans un monde générallement chaud et calme. Trois divisions paléobiogéographiques caractérisent le Passage Marin de l'Ouest Interieur d'Amérique du Nord durant la plupart du Crétacé: une Sous-province Tempéreé-froide de L'intérieur Nord; une Sous-province Tempéreé-douce de L'intérieur central; et une Sous-province Tempéreé-chaude de L'intérieur Sud. Au sud de cette région on retrouve le Golfe Sub-tropical, la Sous-province de la Côte Atlantique et la Province Tropicale des Antilles. Les donneés stratigraphiques révèlent cinq cycles eustatiques du troisième ordre qui ont innondé l'intérieur de l'Amérique du Nord durant le Crétacé. Pour chaque cycle, la distribution des unités paléobiogéographiques a été dramatiquement altéreé à l'intérieur d'un intervalle de un à deux Ma durant une transgression marine maximale. les pics de transgression étaient associés avec des changements paléocéanographiques soudains invoquant; un réchauffement et une amélioration climatique, une normalisation de la salinité et des fluctuations rapides entre des eaux bien oxygénées et des évènements anoxiques. Durant ces intervalles de un à des Ma on note des migrations nordiques importantes de la part des *organismes sub-tropicaux – jusqu'à 1500 milles à l'intérieur de l'ouest-central Canadien; et d'autre part des biotopes des récifs tropicaux pénétrant dans le sud des Etats-Unis. Ces phénomènes se traduisent par des incursions rapides vers le nord des unités biogéographiques sub-tropical et tempéreé-chaude. Celles-ci ont été suivit par une émigration sud aux distributions normales. Des évènements d'extinction majeures ainsi que des périodes d'évolution rapides entre les taxons marins sont fréquemment associés avec ces incursions. Les centres endémiques majeurs et les taux d'évolution les plus rapides au niveau des mollusques du Crétacé de l'Amérique du Nord sont observés à l'intérieur des écotones paléobiogéographiques.*

INTRODUCTION

The widely held concept that ancient paleobiogeographic units – provinces, regions, and realms – were static to slowly shifting, unusually broad divisions of the global biota is not defensible from detailed regional studies (e.g., Pleistocene to Recent biogeographic changes), nor from theory generated by plate tectonics, paleoceanography, paleoclimatology, and modern ecology. The continuous restructuring of continents and ocean basins has produced major barriers and pathways to biotic distribution within a few million years; global sealevel fluctuations reaching hundreds of meters have alternately drowned and exposed large portions of the Earth's continents. Such eustatic changes have greatly altered habitat distribution, migratory pathways, and global climate within 10 Ma intervals – the scale of third-order tectonoeustatic cycles (Vail *et al.*, 1977). These earthbound forces, and extraterrestrial influences on climatic change, should have produced profound short-term shifts in the distribution of the world biota within each geologic period.

Further, biogeographic divisions of the global biota are large-scale ecological units (Kauffman and Scott, 1976), composed of interacting and at least loosely structured communities; as such they should be sensitive to, migrate with, and change niche size relative to shifts in major environmental factors through time. In particular, regional shifts in the large-scale ecotones that mark competitive, ecologically disrupted boundaries between biogeographic units should be recognizable in the fossil record. A prediction can be made that paleobiogeographic units of all ages were highly dynamic, as they were during Pleistocene to Recent glacial and interglacial cycles.

Why, then, the seemingly great discrepancy between the majority of ancient paleobiogeographic reconstructions and the modern distribution of biotas? For example, the majority of papers in Hallam (1973) and Hughes (1973) portray a Phanerozoic world partitioned into a relatively few, broadly distributed biogeographic units, usually "realms" and "provinces" applied inconsistently by various authors to divisions of approximately the same magnitude, and imply that these units were relatively stable over 10 to 35 million year intervals (one-third of a geologic period). Compare these concepts with the Pleistocene to Recent biogeographic divisions of the global marine ecosystem (e.g., Ekman, 1967; Coomans, 1962; Hall, 1964; Addicott, 1966, 1969; Hazel, 1970; Culver and Buzas, 1981a, 1981b; 1982a, 1982b, among many papers on the North American margins). Was the ancient oceanographic-biotic system really that distinct from the modern systems? Theoretically, the only real biogeographic distinctions between the geologically atypical, regionally extensive, glacial intervals (including the Recent) and the more prevalent warm, equable, Phanerozoic climates characterized by higher sea-level stand, should be related to: (a) plate arrangements, affecting distribution of both landmasses and marine systems; and (b) the generally broader Phanerozoic thermal gradient during non-glacial intervals. The latter predictably would result in warmer, more extensive oceans, lacking cold polar zones, and thus broader and somewhat fewer latitudinally distributed, thermally regulated, climatic zones (e.g., restricted to Cool Temperate-Tropical climatic zones of today's oceans). Even these predictable differences do not explain the great discrepancy between, for example, the number of paleobiogeographic divisions plotted for Ordovician trilobites (Whittington, 1973), Silurian brachiopods (Boucot and Johnson, 1973), or Cretaceous cephalopods (Stevens, 1973; Matsumoto, 1973) and the number of modern biogeographic divisions or predictions made for Phanerozoic biotas based on Holocene biogeographic distributions.

Kauffman (1973) addressed many of these problems and identified three important discrepancies between modern and ancient biogeographic analyses: (1) lack of consistency in the definition of paleobiogeographic divisions among Phanerozoic analyses, and between the Phanerozoic and Recent biotas. The criteria used for definition of modern biogeographic units are not consistently applied to analyses of Phanerozoic biotas (*e.g.*, degree of internal endemism, and percent of species crossover at biogeographic boundaries). Even the well defined terminology of modern biogeographic units is inconsistently applied to Phanerozoic distributions (realms, regions, provinces, subprovinces; see Ekman, 1967; and guidelines for quantification by Coomans, 1962; Hazel, 1970; Kauffman, 1973; and Culver and Buzas, 1981a, 1981b; 1982a, 1982b). Without consistency in the definition and classification of modern and ancient biogeographic units, their dynamic changes in space and time cannot be documented.

(2) It is common practice among paleontologists to define paleobiogeographic units based on only one phylum, class, or order of fossil organisms, and more commonly, on only selected taxa (usually genera) within that group. Obviously, emphasis on cosmopolitan eurytopic taxa (e.g., many cephalopods) will give quite a different biogeographic picture than plots for the same time period based on ecologically restricted, stenotopic taxa (e.g., the reef biota). Multitaxial biogeographic plots, such as those that can now be constructed for the marine biotas of the North Atlantic margins (ref. cit.), or at least plots based on all genera or species within a major class or phylum (e.g., Hazel, 1970; Kauffman, 1973; Culver and Buzas, 1981a, 1981b, 1982a, 1982b), are mandatory if paleontologists hope to integrate modern and ancient biogeography, and study the dynamics of paleobiogeographic change.

(3) The stratigraphic resolution of most paleobiogeographic plots is insufficient to show the dynamic changes that predictably should characterize biotic distribution through time. The predominant method of authors in Hallam (1973) and Hughes (1973), for example, is to plot the distribution of taxa within

intervals representing one-third of a geologic period, i.e., 10 to 35 million year accumulations of data. Yet many factors of the global environment that directly affect regional patterns of biotic distribution have a smaller periodicity; e.g., third-order tectonoeustatic fluctuations which emplace and remove extensive epicontinental seas from the craton average 5 to 10 Ma in duration; major biogeographic changes within such cycles may be abrupt. Studies in the Cretaceous of North America indicate that latitudinal shifts in the northern boundaries of single paleobiogeographic provinces of over 1500 miles have taken place within a 2 Ma interval, dated radiometrically (e.g., Late Cenomanian-Early Turonian). Many large-scale climatic cycles have a shorter periodicity, and even the 21,000, 42,000 and 100,000 year Milankovitch-like cycles of the Mesozoic and Cenozoic can be shown to have caused major latitudinal changes in biogeographic distribution during certain intervals. Tectonic and other paleogeographic controls on regional migration and distribution of organisms can certainly act within 10 Ma intervals.

In a stage by stage global paleobiogeographic analysis of all Cretaceous bivalve genera employing measurements of percent endemism in defining and classifying biogeographic units, Kauffman (1973) demonstrated that, even with data from a single major class of Mollusca, it was possible to divide the Cretaceous world into a predictably large number of discrete paleobiogeographic units and to plot their dynamic changes through time within 5 Ma or shorter intervals. In this study, three realms, three regions, seven provinces, and 12 subprovinces of the Cretaceous, representing Cool Temperate to Tropical climatic zones, were identified and their changes plotted through time relative to plate tectonic and tectonoeustatic controls. Based on modern patterns of biogeographic distributions for Mollusca (e.g., Hall, 1964), these were predictable numbers and size-ranges for biogeographic units in the Cretaceous, with its warmer, more equable climates and broader temperature gradients which lacked cold climatic zones around the poles. The origins, spread, decline and extinction of Cretaceous paleobiogeographic units, as defined on percent endemism within each unit through time, were found to be primarily related to plate tectonic control on ocean history, to dispersal and migration of marine organisms, to relative isolation of large gene pools across expanding or contracting oceans, and, thus, to relative development of endemic biotas. These biogeographic patterns were secondarily modified by major tectonoeustatic changes linked to the history of sea-floor spreading. Whereas this study established a new methodology for paleobiogeographic analysis, with important links to modern analyses, it only documented the broad patterns of change for Bivalvia in Cretaceous paleobiogeographic units at 5 Ma intervals, on the average, and identified major causes for change.

This paper explores, in detail, some of the ideas laid down in my 1973 paper, within the great Western Interior Cretaceous epicontinental seaway of North America and the adjacent Gulf Coast and Caribbean basins. Emphasis is placed on interpretation of the dynamics of paleobiogeographic change and on factors controlling major shifts in biotic distribution within the basin. Further, the effects of large scale biogeographic changes, and their causes, on patterns of evolution are documented for several Cretaceous molluscan groups. These analyses have been made possible because of the immense stratigraphic and paleobiologic data-set for this basin available from the works of many students and colleagues in the University of Colorado Cretaceous Basin Analysis Research Group. The high-resolution stratigraphic standard that we have collectively developed for the Western Interior Cretaceous basin is unparalleled, and makes possible the dissection of biogeographic and evolutionary patterns within the basin in the context of a very detailed and accurate matrix of geologic time.

GEOLOGY AND OCEANOGRAPHY OF THE WESTERN INTERIOR CRETACEOUS SEAWAY

Introduction

At peak flooding, the Cretaceous seaway of Western Interior North America extended from Arctic Canada and Alaska south to the Gulf of Mexico, with probable intermittent connections to the Hudson's Bay region (Fig. 1; Williams and Stelck, 1975; Kauffman, 1977a), approximately 3000 miles (4800 km). Shoreline deposits of Minnesota (Bergquist, 1944; Cobban and Merewether, 1983) and central Utah (Ryer, 1977)

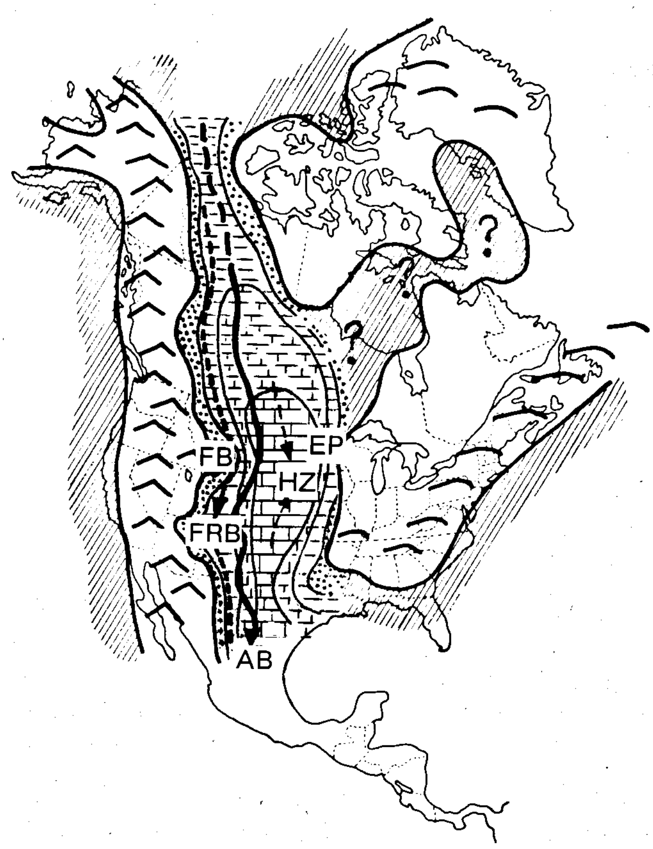

Figure 1. Extent of the Western Interior Cretaceous Seaway, and major facies distribution patterns, within each of the four major tectonic zones of the basin during peak Lower Turonian eustatic rise and transgression. Modified from Kauffman (1969), and Williams and Stelck (1975, Fig. 5). Key: *AB*-Axial Basin; *EP*-Eastern Stable Platform; *FB*-Foreland Basin; *FRB*-Forebulge zone; *HZ*-Hinge Zone.

suggest a maximum width of nearly 1000 miles (1620 km). The size and shape of the seaway changed in response to tectonoeustatic, tectonic and sedimentologic processes (e.g., delta-building). The major elongate trough of the seaway occupied a tectonically generated foreland basin (Price, 1973; Jordan, 1981). To the west lay the great Cordilleran thrust belt, associated with numerous intrusive bodies, and with volcanic centers localized in Idaho-Montana and New Mexico-Arizona. To the east lay the broad, planed, stable cratonic platform. The sedimentary basin was asymmetrical both in terms of subsidence and sedimentary thickness, and in terms of paleobathymetry (Fig. 2; Kauffman, 1977a). In an east-west transect, the Western Interior Cretaceous Basin was divisible into four tectono-sedimentologic "provinces" (Fig. 2; Kauffman, 1977a): (1,2) A pair of western to west-central, rapidly subsiding troughs, separated by a forebulge zone, with a steep western slope and moderately sloping eastern edge: these are (1) the tectonically generated western foreland basin containing thick coarse clastics (Jordan, 1981), and; (2) an axial basin, the zone of maximum subsidence and the deepest part of the seaway at maximum flooding; (3) an east-central, temporally shifting, tectonic hinge zone between the foreland basin and stable platform, characterized by episodic block uplift or isostatic flexure, intermittent basin-swell topography, and rapidly changing fine-grained marine facies cut by complex regional disconformities; and (4) a stable eastern platform zone characterized only by broad subsidence-uplift episodes, widespread uniform, fine-grained clastic and carbonate facies, and shallow, mainly photic water depths.

The seaway was initially flooded from the north end in the Aptian Stage; during the Aptian-early Late Albian stages an extensive northern arm of the seaway (Fig. 3; McGookey *et al.*, 1972; Williams and Stelck, 1975), and a minor southern arm encroached slowly and irregularly into the basin, meeting in middle Late Albian time in central and southern Colorado (the Kiowa-Skull Creek eustatic cycle; Kauffman, 1969, 1977a). After a brief, partial, Late Albian retreat, the two arms of the seaway once again joined in latest Albian-earliest Cenomanian time and remained as a continuous marine system between the proto-Gulf of Mexico and the Circum-Boreal Seaway for nearly 35 Ma, draining from the interior for the last time in the Middle Maastrichtian ("Fox Hills time"; Waage, 1968) but with a remnant arm persisting into the Middle Paleocene (Cannonball Sea). During latest Albian-Middle Maastrichtian time, however, five major third-order tectonoeustatic cycles and numerous important fourth-order transgressive-regressive cycles altered the shape, bathymetry, and sedimentational patterns of the basin (Kauffman, 1969, 1977a); all third-order and some fourth-order cycles can be linked, through precise biostratigraphic-geochronologic correlations, to global tectonoeustatic sea-level changes (Kauffman, 1977a, 1979; Hancock and Kauffman, 1979; Vail *et al.*, 1977). Peak rises of sea-level recording third-order cycles in the Western Interior basin occurred in the middle Late Albian (Kiowa-Skull Creek Cycle), the middle Early Turonian (Greenhorn Cycle), the Lower Coniacian-Late Santonian (Niobrara Cycle, containing four discrete fourth-order cycles), the late Early Campanian (Claggett Cycle), and the middle Late Campanian stages (Bearpaw cycle) (Kauffman, 1977a). Fourth-order cycles thought to be related to smaller sealevel changes, or stillstand events, are expressed as smaller

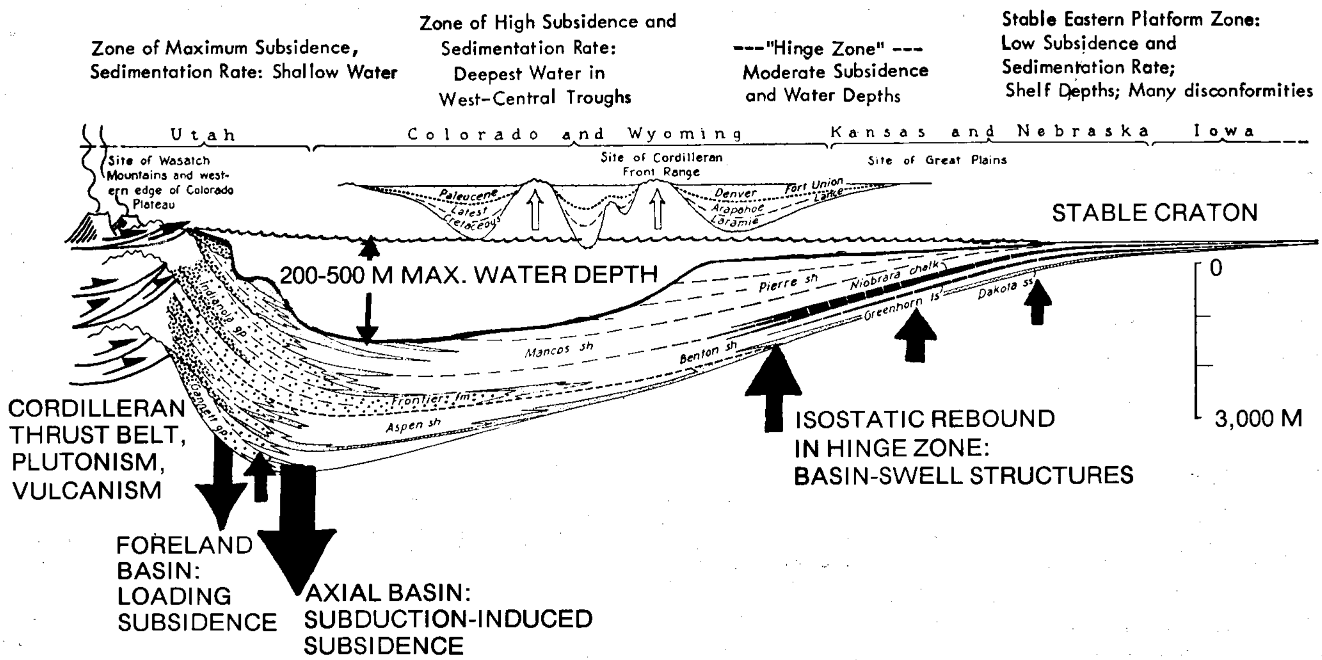

Figure 2. Generalized structural and stratigraphic cross-section through the Western Interior Cretaceous Basin (modified from Kauffman, 1977a), modeled after a peak transgressive phase and eustatic high-stand, showing the major structural divisions of the basin, sediment thicknesses and facies characteristic of each division, and relative paleobathymetry. Position, direction, and size of arrows indicate relative thrusting, subsidence, and uplift at the western margin and within the basin during periods of eustatic rise.

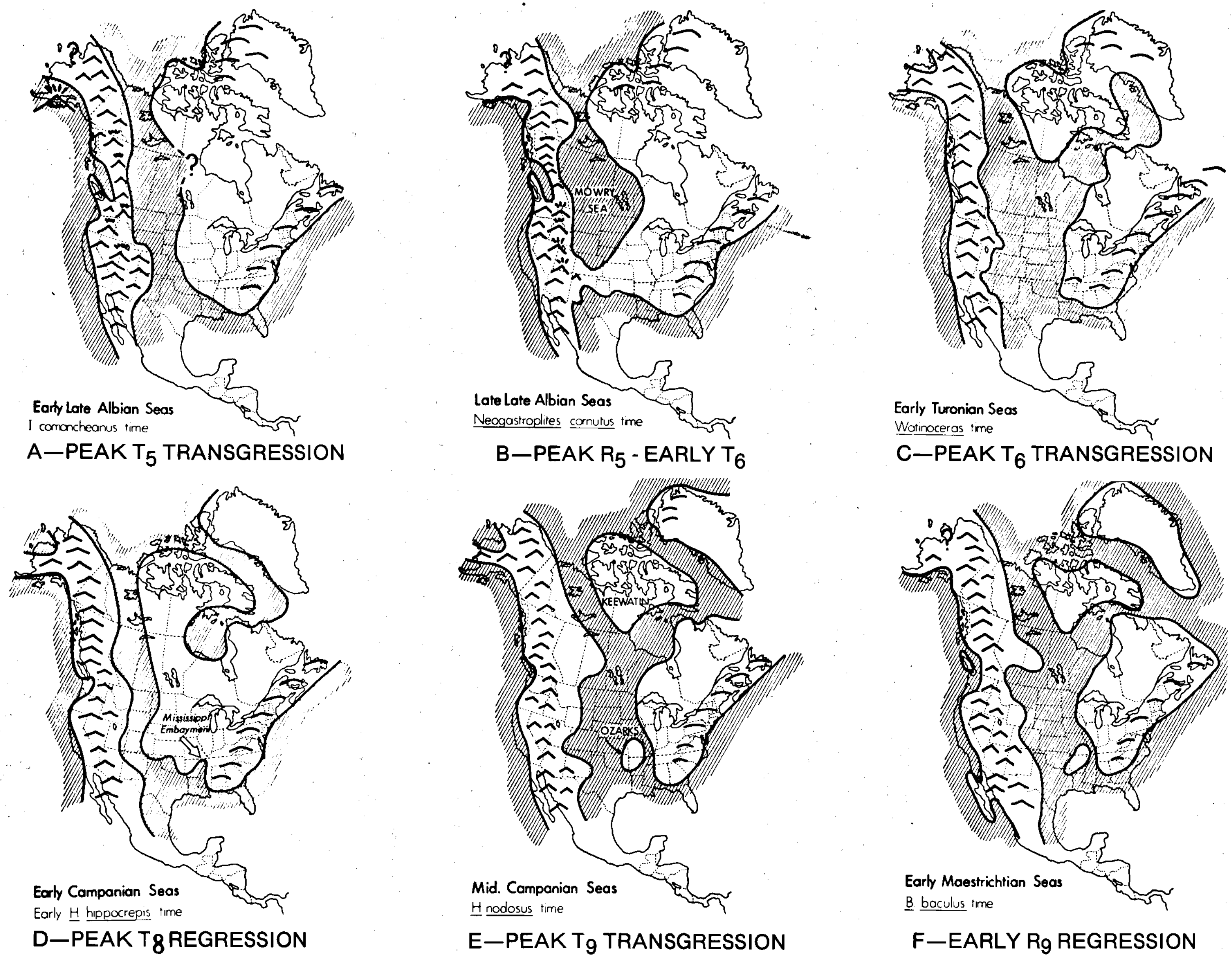

Figure 3. Generalized maps of North America showing extent of Western Interior Cretaceous Seaway during major third-order eustatic fluctuations (transgressions and regressions, utilizing Kauffman's 1977a nomenclature), in temporal progression from A – F (oldest to youngest). Maps from Williams and Stelck, 1975, slightly modified.

regional strandline fluctuations, progradational events, and/or regional disconformities. These sealevel fluctuations, coupled with related tectonic modification of the foreland basin, exercised the principal control on climate and biogeographic distribution in the Western Interior Seaway through time.

Tectonoeustatic sealevel changes within the Western Interior Basin are expressed as regionally correlative migrations of strandlines (e.g., Weimer, 1959, 1960; Gill and Cobban, 1973) and basinal sedimentary packages which, when fully preserved, consist of an upward-fining and/or more calcareous facies-suite overlain by a lithologically very similar, but reversed, upward-coarsening facies-suite (Figs. 5, 6, 9; Hattin, 1964; Kauffman, 1967, 1969, 1977a). Collectively, the strandline migrational surfaces (disconformities) and the sediment-suites comprise the marine cyclothem for each fluctuation of sealevel. Internally, each cyclothem bears lithologic, paleobiologic, and geochemical evidence of major changes in climate and currents, water stratification, temperature, and chemistry of the epicontinental sea which had a profound effect on the marine biota and its patterns of distribution through time.

Detailed interpretation of the eustatic, tectonic, sedimentologic, and ecologic-paleobiogeographic evolution of the Western Interior Cretaceous Seaway and the correlation of these events regionally to establish the magnitude of causal phenomena, demand a complex and refined system of high-resolution stratigraphy with world-wide application. We are fortunate that the Cretaceous System of correlation established for the Western Interior Seaway is perhaps the most refined anywhere in the world, combining isochronous surfaces of over 600 layers of volcanic ash and other "geologically instantaneous" events with a rapidly expanding bank of geochronologic data (> 50 K-Ar dates/40 Ma), an emerging and highly precise stable-isotope chemostratigraphy, and a biostratigraphic system of interval and assemblage biozones with resolution averaging 0.25-0.33 Ma/zone for most of the Cretaceous sequence.

Tectonic Framework

The Western Interior epicontinental sea occupied an Andean-type foreland basin, the origin and structural history of which was controlled by: (a) plate-tectonic activity, timing and intensity along the subduction zone of the Pacific coast of North America; (b) the timing and magnitude of regional compressional (thrust) tectonics in the western Cordilleran orogenic belt; and (c) the structural integrity of the crust in front of the Cordilleran thrust belt. All of these factors worked in concert to shape the Western Interior Basin, the history of epicontinental marine incursions, and biogeographic evolution of the seaway.

Figure 2 shows the major tectonic divisions of the basin (after Kauffman, 1977a) during the Cretaceous, from west to east: (a) the tectonically active, topographically elevated western belt of thrusting, intrusion, and vulcanism, which episodically provided immense amounts of terrigenous clastic sediments to the rapidly subsiding western trough of the seaway. Price (1973) and Jordan (1981) demonstrated that this trough was formed by crustal loading through eastward pileup of thrust plates, and accumulation of thick, predominantly coarse-terrigenous clastic sequences east of the thrust belt. Coastal-plain and predominantly shallow-water marine sequences characterized the western margin of the epicontinental sea, indicating that subsidence responded in proportion to tectonic plus sedimentologic loading of the crust. (b) The west-central trough along the basin-axis in which, regionally, the thickest accumulation of marine sediments developed, generally medium to fine-grained clastics (McGookey et al., 1972, Figs. 31, 32, 35, 43). This was the deepest part of the basin, based on slope analysis and bathymetric indicators among the biota, during sealevel rise and highstand. Rapid subsidence of the basin along its axis, with subsidence outstripping sediment loading, is thus indicated; this center of subsidence was outboard of predicted basinal development due to crustal and resultant sediment loading (Jordan, 1981), and thus a distinct, more remote mechanism for mid-basin subsidence must be called upon, possibly, some kind of a "drag effect" related to rapid, shallow plate-subduction originating at the Pacific margin of North America. Separation of the thick sedimentary sequences of the foreland trough from those of the basinal axis by a zone of thinner sedimentary sequences suggests some kind of foreland-bulge between them. Sedimentation patterns indicate that subsidence throughout these depositional basins was intermittent and separated by times of basin filling.

(c) The broad, migrating, east-central tectonic hinge zone (Fig. 2) bounded on the west by a moderately inclined slope descending into the axial basin, along which rapid facies change took place from thin sequences of eastern platform carbonates and clays cut by numerous regional disconformities to thick westward sequences of clays, silts and sands lacking major disconformities (Fig. 2; and McCookey *et al.*, 1972, Fig. 43). Subsidence was moderate and episodic west of the hinge zone, and occurred sporadically at very low levels on the eastern platform. The hinge zone was a region of tectonic adjustment to pulses of subsidence and loading in the basins to the west. It was characterized by periodic development of block uplifts separated by smaller basins. Analyses of stratigraphic thicknesses across this hinge (from Hattin, 1962, 1964, 1965, 1975, 1982, for Kansas; Kauffman, 1969, 1977b; Kauffman *et al.*, 1969; Scott, 1969; and Cobban and Scott, 1972 for Colorado), shows thinning of certain stratigraphic intervals, but not others, across basement blocks of the hinge zone; this dates their movement as correlative with episodes of thrusting to the west and with times of eustatic sealevel rise (Fig. 4).

(d) The tectonically stable platform occupied the eastern one-third of the seaway. During maximum transgression the seaway inundated the stable craton and the Transcontinental Arch. Subsidence was low and episodic, affecting broad areas, and sedimentation was characterized by slow accumulation of pelagic carbonates and fine-grained terrigenous clastics in low-energy but predominantly photic marine environments. Coarser clastics (sand) were thin and mature, and restricted to very nearshore facies.

Many aspects ofthe tectonic history in the Western Interior Basin may have affected the geographic distributional patterns of Cretaceous marine organisms. (a) Rates, timing, and magnitude of subsidence events controlled water depth, water mass distribution, and the current systems involved in dispersal and the development of habitats for marine organisms. Active subsidence and deep water occurred only during eustatic rise of sealevel; basin filling, reduced subsidence, and a predominance of shallow water habitats, characterize regression and eustatic fall. Varying patterns of subsidence along the basinal axis determined north-south continuity of depth-zones and water-masses. (b) The size and shape of the basin and relative constriction of its apertures (Williams and Stelck, 1975, Text-figs. 3-6) influencing current and tidal circulation, were controlled by sealevel changes, crustal shortening, block-uplift of large parts of the basin, and/or emplacement of tectonic blocks in basinal apertures. (c) Rainfall and evaporation levels in the Western Interior seaway controlled surface salinity and were affected by episodic development of extensive mountain ranges along the western side of the basin through thrusting and uplift. These elevated ranges caused extensive updrafts, air turbulence, and greater precipitation than to the east. Increased runoff from these ranges intermittently produced brackish surface-layers on the seaway, restricting planktonic dispersal. Intermittent reduction of those ranges would have greatly altered climatic patterns toward drier phases. Similarly, episodes of massive volcanic eruptions potentially altered the atmosphere of the Western Interior in terms of cloud-cover, heat-penetration, and thus annual temperature and rainfall – critical factors in the Cretaceous history of biogeographic dispersal as they are in modern marine environments (Kauffman, 1975). Over 600 volcanic eruptions are recorded in middle and Upper Cretaceous marine

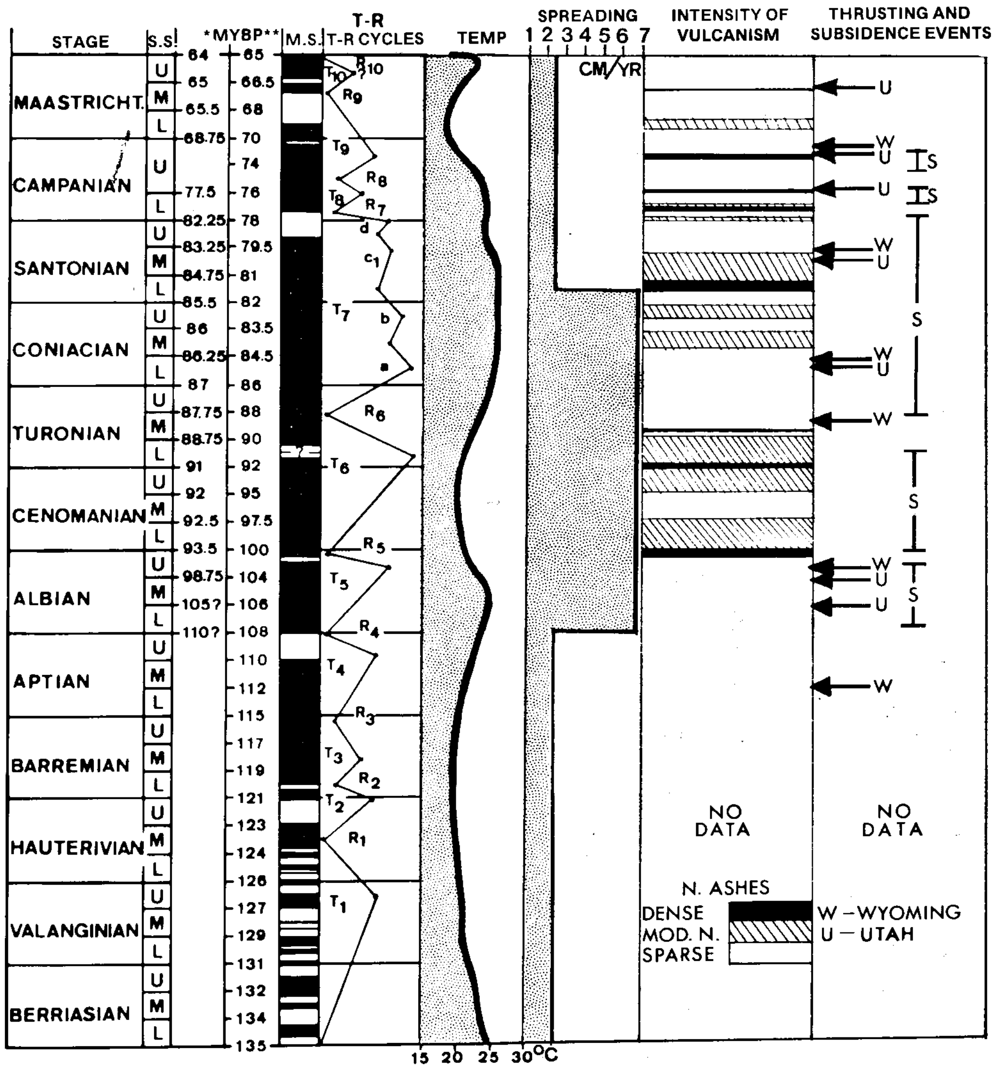

Figure 4. Geochronologic and magnetostratigraphic dating of global sealevel changes; third-order transgressive-regressive (T-R) epicontinental cycles (from Kauffman, 1977a); average marine temperature fluctuations (averaged from data in Kauffman, 1977a); Atlantic and Pacific half-spreading rates averaged (Larson and Pitman, 1972; Sheridan *et al.*, 1982); episodes of intense (black) and moderately intense (striped) volcanism, measured by number and magnitude of volcanic ash events (partially from Kauffman *et al.*, 1976); initiation of major thrusting (arrows) in Utah (U) and Wyoming (W) (data from Villien and Kligfield, pers. commun., 1984, and Wiltschko and Dorr, 1983, respectively); and times of most active basin subsidence (S), determined stratigraphically, in the Western Interior Seaway. Note correlation of active tectonism, subsidence, and volcanism with periods of active plate spreading and global sealevel rise, as contrasted to periods of relative tectonic quiescence during sealevel fall. Generalized time scales from Kauffman (Western Interior Seaway, left column, 1977a) and Van Hinte (global; right column, 1976).

strata of the Western Interior by 0.1 cm-3 m thick ashes and bentonites. (d) Episodes of thrusting and uplift are marked by massive influx of terrigenous clastics, and with them greater turbidity, varying chemistry, and fluctuating water-depths affecting biotic migration over broad areas.

From these observations a synthetic theory for the dynamics of the Western Interior foreland basin can be developed and applied to the interpretation of Cretaceous paleobiogeographic patterns, as follows. Acceleration of rates of seafloor spreading in the Cretaceous was associated with development of topographically positive regions on the ocean floor, causing global tectonoeustatic sealevel rise up to 300 metres and widespread, synchronous, epicontinental transgression. Active spreading also correlated with increase in subduction rates along the Pacific boundary of North America. This activated compressional deformation in less stable, inboard portions of the craton, resulting in the development of an asymmetrical foreland basin bounded on the west by linear fold and thrust belts, intrusive igneous bodies, and active vulcanism. Coincident subsidence, eustatic drowning and greatly increased sedimentation in the Western Interior epicontinental basin was predictable. Water-depth in this seaway depended upon rates of eustatic rise and basin subsidence balanced against rates of sedimentation. High-resolution correlation of events in the Western Interior Cretaceous Basin clearly supports this theory (Fig. 4). Periods of active Cretaceous plate spreading (Rona, 1973, Pitman, 1978) bracket both the interval of major thrusting, uplift, and volcanism in the Western Interior Basin, and the interval of greatest eustatic drowning, subsidence, and marine sedimentation (Kauffman *et al.*, 1979b, Fig. 2). All major thrusting events (dated by large-scale movement on thrusts and resultant sedimentary events), and the majority of episodes of intense volcanism (measured by numbers, spacing, thickness and distribution of volcanic ashes) are precisely correlative to episodes of marine transgression and eustatic rise (Fig. 4). Episodes of rapid basinal subsidence preserving the thickest coarse clastic sequences in the foreland trough, and continuous transgressive sediment packages recording maximum water depth in the axial basin, are all associated with sealevel rise and transgression. Contemporaneous subsidence in the central basin exceeded sedimentation, protecting fining-upward transgressive sequences from erosion and creating the deepest water along the basinal axis; consequently clastic wedges emanating from the western thrust belt during sealevel rise do not cross the basinal axis (see McGookey *et al.*, 1972, Fig. 43). The relationship between regional tectonic activity, active volcanism, extensive basin subsidence, rapid sedimentation, and sealevel rise holds for all five of the major third-order tectonoeustatic pulses in the Western Interior Cretaceous (Fig. 4).

The second part of the theory predicts that during regressive phases of each third-order eustatic cycle, slowing or cessation of seafloor spreading and subduction resulted in low levels of epicontinental tectonism – thrusting, folding, subsidence, intrusion and vulcanism – initiating destruction of Cordilleran ranges through erosion. Falling sealevel, epicontinental regression, and slowing of tectonically generated basinal subsidence resulted in filling of the epicontinental basin with progressively coarser sediment; basinal subsidence during regression was primarily related to sediment-loading. The history of the Western Interior Basin supports this theory. No major thrusting or intrusive episodes, and less than 25 percent of the volcanic ash deposits are associated with regional marine regression and eustatic fall. Rates of sedimentation near the thurst belts generally decline, but the central part of the basin fills with sediment to the point where large scale progradational events produce sand bodies that cross the former sites of the foreland and axial basins without reflecting any topographic depression during regression (Fig. 2; and McGookey *et al.*, 1972, Fig. 43).

This tectonic theory predicts, therefore, that: (a) immigration of taxa into the Western Interior Basin from both northern Cool Temperate and southern Warm Temperate to Subtropical paleobiogeographic sources, (b) establishment of broad biogeographic ecotones, and (c) rapid shifts in paleobiogeographic boundaries within the basin, would be possible mainly during transgression and eustatic highstand. During these intervals the size and depth of the seaway, and the diversity and quality of paleoenvironments would be favorable for development of diverse biotas, high productivity, and establishment of migratory pathways at several levels within the marine water column. This favored widespread migration of permanent plankton, nekton, and of the planktotrophic larvae of many benthic marine organisms. Paleobiogeographic data presented subsequently wholly supports this interpretation.

Conversely, eustatic lowering produced regressive phases of the Western Interior Seaway, constriction of basinal apertures, basin filling, decrease in basinal size, restriction and reduction of both depth-controlled and spatially-controlled niches for marine organisms. These greatly diminished opportunities for immigration and/or spread of biotas from adjacent biogeographic units, especially those of deep- and warm-water environments. Regressive phases of basinal development would thus favor expansion of endemic shallow-water taxa with Temperate zone affinities, and with preferences for clastic substrates. Regional retreat of southern paleobiogeographic assemblages and increased endemism during eustatic fall are predictable and observed within the basin.

Patterns of Sedimentation

Patterns of sedimentation in the Western Interior Seaway, depicting the evolution of pelagic and benthic environments and niche diversity, were closely linked to both regional tectonic and tectonoeustatic controls (Kauffman, 1977a). At peak Cretaceous flooding (e.g., Early Turonian; Coniacian-Santonian) all major marine facies were developed in the basin; niche diversity was high and many habitats were extensively developed – a favorable setting for immigration and proliferation of biotas having diverse paleobiogeographic origins. Kauffman (1967, 1969, 1977a) described and traced 12 major marine facies through five third-order tectonoeustatic cyclothems of the Western Interior Basin, and showed them to contain diverse, benthic, marine paleocommunities of both northern and southern origin. Detailed biostratigraphic and geochronologic correlation of transgressive and regressive peaks of Western Interior cyclothems to similar peaks in Western Europe and other Cretaceous areas of the world by Hancock and Kauffman (1979) and Kauffman (1979) proves their tectonoeustatic origin.

Kauffman (1967, 1977a) suggested that the basic sedimentation model for a single tectonoeustatic cycle in rapidly subsiding basinal settings of the Western Interior Seaway was that of a symmetrical cyclothem (Fig. 5). This model contains 12 major marine and marginal-marine lithofacies arranged in an upward-fining sequence, from nearshore sands to offshore pelagic carbonates, during transgression (eustatic rise); essentially the same facies-suite occurs in reverse order (upward coarsening) during regression and eustatic fall. The model proposes diachronous transgressive and regressive disconformities bounding each cyclothem shoreward, with gradual shoreward loss of pelagic carbonates and shales but lateral retention of the basic symmetry of the cyclothem. In this eustatic model points of maximum transgression of the eastern and western strandline facies correlate precisely with the point of maximum development of pelagic carbonates in the upward-fining basinal sequence in both third- and fourth-order cycles.

Several modifications of this model have been suggested by subsequent work, in each tectonic zone of the basin. (1) Along the western margin of the seaway and in the rapidly subsiding foreland basin the cyclothems are preserved in thick sequences of coarse, continental, marginal-marine, and nearshore marine terrigenous sediments cut by multiple disconformities mainly developed across the top of progradational units. Thin, fossiliferous marine shaley units represent times of peak-transgression and eustatic rise (Ryer, 1977). Third-order cyclothems of this region are broadly symmetrical, but are frequently interrupted by major strandline reversals, representing upward-coarsening progradational events (Ryer, 1977). These strand migrations comprise asymmetrical fourth-order cyclothems with marked transgressive disconformities, little or no preserved transgressive sediment, and thick regressive sequences. Fourth-order cycles

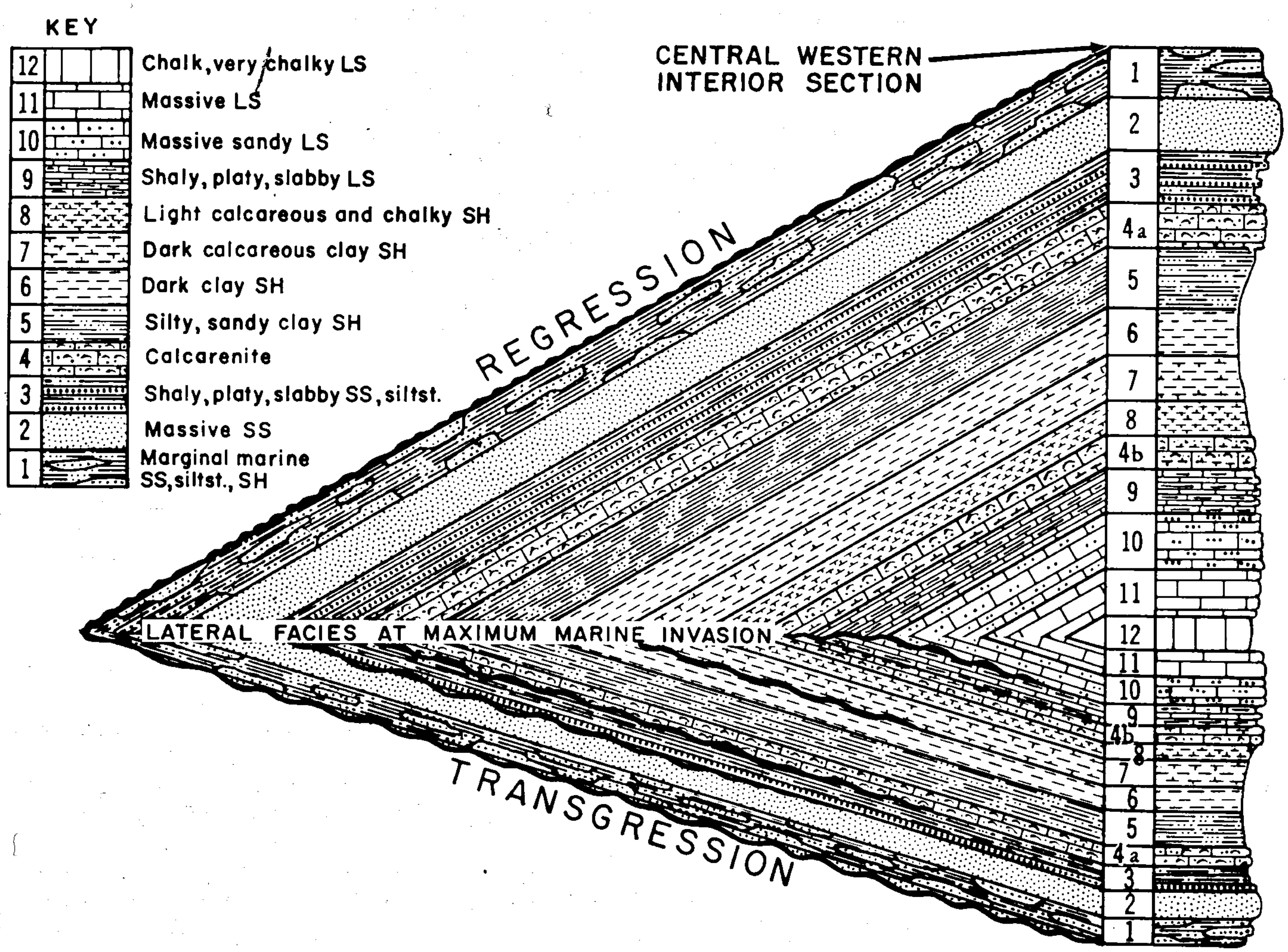

Figure 5. Generalized model of a symmetrical Cretaceous cyclothem, reflecting deposition during a third-order tectonoeustatic fluctuation, in the center (right) and shallow marginal platform (left) of a hypothetical epicontinental sea (based on center to eastern margin transect of Western Interior Cretaceous Basin). Modified after Kauffman (1969, 1977a) in which the upward-fining transgressive facies (1-12) and upward-coarsening regressive facies (12-1), are defined in detail as preserved in the axial part of the Western Interior Basin. Note shoreward-basinward diachronism of facies during transgression-regression, bounding disconformities, and concentration of intra-cycle disconformities on transgressive hemicycle.

are most extensively developed on third-order regressive (eustatic) hemicycles. Some fourth-order cyclothems also appear to be linked to eustatic fluctuations or still-stand events (e.g. progradational sequences); others were caused by regional tectonic, subsidence, and sedimentation events.

(2) In the deep, west-central, axial part of the basin the thickest and most diverse sequence of marine sediments is preserved (McGookey *et al.*, 1972, Figs. 30-35, 43) and characterized by dark silty clay and calcareous clay-shales, intercalated with thinner distal (basinal) extensions of pelagic carbonate units from the eastern shelf during peak transgression, and with basinal extensions of prograding sand-dominated facies from the west during regression. These cyclothems are basically symmetrical with upward-fining (and/or more calcareous) facies during eustatic rise and transgression, and with upward-coarsening sequences during regression and eustatic fall. The cyclothems become somewhat asymmetrical on the eastern flank of the basin where regional disconformities of small duration cut mainly the transgressive sequences, increasing in magnitude eastward over the hinge zone and onto the stable platform. It is from Cenomanian through Santonian rocks in this region that Kauffman (1967, 1977a) developed the cyclothemic model for the Western Interior Cretaceous Basin (Fig. 5). The symmetry of the cyclothems in the axial part of the Western Interior Basin is strong evidence for rapid subsidence during transgression which exceeded tectonic and sediment loading, dropping transgressive sequences rapidly into deep-water zones before they were extensively eroded. However, even the most symmetrical mid-basin cyclothems have significantly different coarse-clastic sequences bounding them. Transgressive sandstones and calcarenites track the transgressive disconformity in a narrow belt of nearshore facies, with few progradational sequences; none of these progradational sequences cross the axis of the depositional basin, and most do not even reach the basinal axis, confirming that this was the deepest part of the seaway during eustatic rise (see McGookey *et al.*, 1972, Fig. 43). Regressive coarse-clastics in the cyclothems, however, are characteristically more abundant and occur as widespread progradational facies which extend across the depositional axes of the basin without significant change, in some cases reaching the hinge zone and eastern platform. This confirms basinal filling during regression and eustatic fall, with subsidence barely keeping up with sedimentation (e.g., McGookey *et al.*, 1972, Fig. 43; Gill and Cobban, 1973).

(3) The east-central tectonic hinge zone of the Western Interior Basin is characterized by extensive facies change and rapid eastward thinning of dominantly fine-grained marine sedimentary sequences (Fig. 2; McGookey *et al.*, 1972, Fig. 43). Sedimentary units comprising transgressive sequences are variable in thickness across the hinge as a result of active basement flexure and block uplift during eustatic rise and, thus, numerous disconformities are developed which cut the sequences on the transgressive hemicyclothems and at peak regression. Thus, the cyclothems are sub-symmetrical, with transgressive sequences significantly shortened by these disconformities but with little change in facies sequences (Kauffman, 1967, 1977a).

(4) The eastern platform zone encompasses one-third of the Western Interior Basin (Fig. 1), and is characterized by thin sedimentary sequences dominated by clayey, silty, and calcareous shales, and by pelagic carbonates deposited in shallow (photic) waters. Thin mature sands abound in the nearshore facies, suggesting limited clastic sources on the broad flat eastern coastal plain. Cyclothems are subsymmetrical near the hinge zone, with thin discontinuous transgressive sequences cut extensively by regional disconformities, bypass surfaces, and condensation zones; third-order cyclothems become asymmetrical shoreward (Hattin, 1975) with nearly complete regressive sequences overlying extensive transgressive (ravinement) disconformities preserving little or no transgressive sediments other than lag deposits. The extensive development of pelagic carbonates composed of diverse calcereous microplankton in photic shelf environments seems unusual. This probably reflects exceptional warmth and clarity of the shallow eastern platform seas during the Cretaceous, and also suggests different ecological ranges for certain Cretaceous calcereous plankton than documented for their modern counterparts. Extensive immigration of Warm Temperate to Subtropical calcereous plankton into the seaway, including the larvae of many benthic organisms, appears to have taken place rapidly across the shallow eastern platform during peak rise of sealevel.

Variations in the development and/or preservation of Cretaceous cyclothems in the basin reflect secondary tectonic, sedimentologic, and oceanographic influences on the expression of global eustatic events, not predominant regional control on development of these cycles. Paleobathymetric analyses and facies distribution within these Cretaceous cyclothems indicate that deep-water migration routes for northern and southern biotas developed in the central and west-central parts of the basin only during eustatic sealevel rise and transgression. Extensive development of pelagic carbonates suggests that peak transgression was characterized over parts of the basin by the immigration of warm water masses, and by increases in salinity and biotic productivity. Changes from fine-grained clastics to pelagic carbonates signals the point of change in water mass and predicts a shift from Temperate to Subtropical climates and marine environments of the upper water column. Favorable benthic habitats expanded during transgression; transgressive events were times of maximum opportunity for immigration and exchange of biotas within the seaway, especially from southern Warm Temperate to Tropical paleobiogeographic units. Conversely, shallowing, cooling, and decrease in salinity characterize regressive facies and eustatic fall; these conditions favored limited colonization by shallow-water Temperate and endemic marine biotas. Southward shift of warm-water paleobiogeographic units is predictable from facies analysis during marine regression.

Paleoceanography of the Western Interior Seaway

Tectonic and sedimentologic patterns within the Western Interior Seaway also reflect major oceanographic fluctuations which exercised primary control on the paleobiogeographic distribution of marine organisms. The most obvious of these are tectonoeustatic changes of sealevel, which caused broad transgressive-regressive migrations of the strand-line, major changes in shape, size, and continuity of the seaway, and alternating episodes of deepening and shoaling. Eustatic effects were greatly enhanced by coincident tectonic activity which exercised strong controls on the orientation, physiography, and paleobathymetry of the seaway. Five major third-order tectonoeustatic cycles (Vail *et al.*, 1977), averaging about 9 Ma in duration, and more numerous fourth-order cycles depicting relative sealevel changes and eustatic stillstand events, characterize the paleoceanographic history of the Western Interior Seaway (Fig. 6). All third-order and some fourth-order cycles have transgressive and regressive peaks which are correlative worldwide within one or two regional biostratigraphic zones of 0.2 to 0.5 Ma duration, proving their tectonoeustatic origin (Kauffman, 1977a, 1979; Hancock and Kauffman, 1979). Widely correlative transgressive peaks in the middle Late Albian (Kiowa-Skull Creek Cyclothem), middle Early Turonian (Greenhorn Cyclothem), Lower Coniacian through Late Santonian (Niobrara Cyclothem; divided into four fourth-order eustatic pulses); late Early Campanian (Clagget Cyclothem), and middle Late Campanian (Bearpaw Cyclothem) are expressed in the centre of the basin by maxima in upward-fining clastic sequences and/or deposition of pelagic carbonates, and marginally as maximum shoreward migrations of the strand line which overprint virtually all regional tectonic, sedimentation, and subsidence phenomena. Hancock and Kauffman (1979, Fig. 5) and others propose maximum middle and Late Cretaceous elevation of sealevel during peak rise in Euramerica as about 300 m.

These large tectonoeustatic fluctuations regulated the paleoceanography of the Western Interior Seaway. During each eustatic rise the following sequence of changes can be generalized from sedimentologic, geochemical, and paleobiologic data. (1) With initial transgression, limited interconnection of separate northern Cool Temperate and southern Warm Temperate to Subtropical water masses, allowed immigration and extensive mixing of northern and southern marine biotas, and established broad biogeographic ecotones documented by the geographic extent of mixing of characteristic northern and southern taxa (Sohl, 1967, 1971; Kauffman, 1967, 1973, 1977a, 1979). Northern taxa migrated as far south as Texas (Stephenson, 1952), and Subtropical taxa as far north as central Saskatchewan (Douglas, 1972; Caldwell and Evans, 1963). The Tropical reef line seems to have shifted north into Texas with each major eustatic rise. (2) Enlargement and progressive deepening of the epicontinental seaway, reflecting eustatic rise, accelerated subsidence and deepening along the basinal axis. Major northern and southern marine currents moved into the Western Interior Basin (Kauffman, 1975), overriding constrictions at the northern and southern apertures of the seaway (narrow necks and shallow sills) that earlier had prevented free circulation of tides, currents, and immigration of many biotic constituents from the Gulf of Mexico and Circumboreal Sea. (3) With widespread flooding and open-marine circulation in the basin around peak transgression, a regional maritime climate developed with warming temperatures, rising surface salinity, and declining seasonality. These changes were accompanied by extensive northern migration of warm waters, and rapid northward shifts of Warm Temperate to Subtropical biotas of the Caribbean, Gulf of Mexico, and southern Western Interior, reflecting rapid, short-term (1 to 3 Ma) changes in watermass distribution, currents, temperature and salinity which occur near the eustatic highstand for each cycle. (4) Coincident draining and shoaling of the Western Interior Basin occurred during eustatic fall and regression (average 4 to 4.5 Ma duration). The size of the basin was reduced, the maritime climate disrupted, and basinal circulation became restricted as barriers to incursion of large currents from the north and south were re-established. With these changes, cooling, greater seasonality, increased rainfall, and decreased surface salinity in the seaway predictably forced warmer water, more normal marine biotas southward toward the Gulf of Mexico and Caribbean, leaving behind more eurytopic Cool- to Mild-Temperate biotas.

This oceanographic model is supported by new geochemical and paleobiological data. Two powerful geochemical tools have been applied recently to the interpretation of water chemistry, climate and temperature in the Cretaceous seaway of North America: (a) state isotope geochemistry, primarily involving the use of carbon ($\delta^{13}C$) and oxygen ($\delta^{18}0$) isotopes to sense temperature and/or salinity levels through time, and (b), along with $\delta^{13}C$ analysis, the use of organic carbon (C_{org}) values to sense original environments of deposition – the preservation of organic carbon is directly related to dissolved-oxygen levels within the water column and benthic substrate. C_{org} level is also a rough measure of biological productivity. Temperature, salinity, and oxygen levels have strong controls on the dispersal of marine organisms, ecosystem structure, and thus on the characteristics of paleobiogeographic units.

Scholle and Arthur (1980) and Pratt (1983; and pers. commun., 1983) generated detailed stable isotope curves for the Western Interior Cretaceous based on $\delta^{18}0$ and $\delta^{13}C$ analysis of carbonate rock fragments and calcite prisms from inoceramid bivalve shells. These curves span the Greenhorn and Niobrara Cyclothems with data largely drawn from the central and eastern part of the seaway. These data (Fig. 6) demonstrate fluctuations in aquatic chemistry of the Western Interior seaway that profoundly affected the dispersal of marine organisms (Fig. 6).

Analyses of oxygen and carbon isotopes show unusually negative values for both $\delta^{13}C_{org}$ and $\delta^{18}0$ through most of the transgressive-regressive history of the seaway, compared to modern marine systems. Negative $\delta^{13}C_{org}$ values range between -25 and -27 (°/oo *vs.* PDB) during all but peak-transgressive phases (eustatic highstand) of basin history. Peak-transgressive values climb slightly to -23 (°/oo *vs.* PDB). $\delta^{18}0$ values range from -7 to -11 during most of the basin's marine history, climbing to -3 to -5 (°/oo *vs.* PDB) at peak-transgression and eustatic highstand. Values around -3 $\delta^{18}0$ are considered to represent near-normal marine (saline) conditions for epicontinental Cretaceous seaways (M.A. Arthur, pers. commun., 1983). Interpreted as temperature, $\delta^{18}0$ fluctuations indicate temperature range and projected values which are much too severe for the biota associated with the samples, so that salinity fluctuations are called upon to explain these values.

Interpreted as a signal of salinity fluctuation, these values suggest slightly to moderately brackish conditions during most of the marine history of the seaway, especially in the upper part of the water-column. A widespread brackish cap probably developed here as a result of internal freshwater runoff which

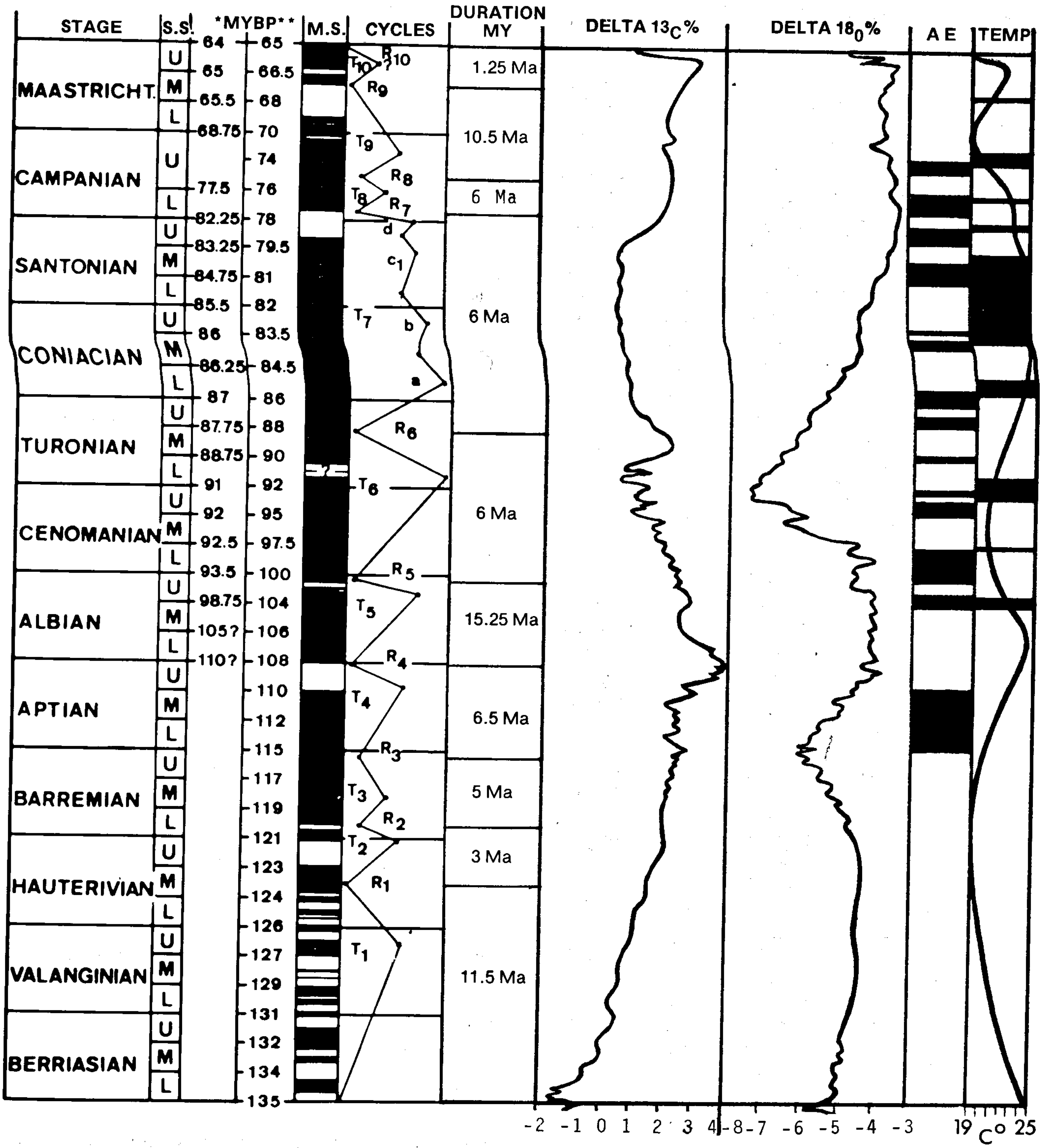

Figure 6. Global third-order tectonoeustatic cycles (T_1-R_1) plotted against magnetostratigraphic and radiometric standards (from Kauffman, 1977a; see explanation, Fig. 4 herein). T_5-T_{10} widely inundated the Western Interior Cretaceous Basin. Note radiometric times of peak transgressive and regressive events, cycle durations, and major paleoceanographic fluctuations as defined by geochemical profiles ($\delta^{13}C_{arb}$, $\delta^{18}O_{org}$). Geochemistry generalized from Scholle and Arthur (1980); Pratt (1983). Right hand columns show anoxic events (AE) and rapid warm-water incursions (TEMP) as black bands, marine temperature curve generalized from data in Kauffman (1977a).

was not offset by tidal and current exchange of normal seawater into the basin. $\delta^{18}O$ isotopes indicate that normal-marine salinity was developed only near eustatic highstand and peak transgression. Consequently, immigration of plankton, nekton, and the planktonic larvae of many normal marine benthic organisms from northern Cool Temperate and southern Warm Temperate to Subtropical subprovinces was greatly restricted during much of the basin's marine history by brackish water in the photic part of the water column. Near peak transgression, isotopic data (Fig. 6) suggest that shifts to normal salinity were relatively rapid, and lasted less than 2 Ma for the Greenhorn and Niobrara Cycles. The rapid normalization of salinity near peak-transgression in the Western Interior Seaway might reflect eustatic rise reaching some threshold point at which warm southern waters were deep enough to overstep barriers to circulation in the southern end of the seaway and thus to flood rapidly into the interior. Oceanographically widespread immigration of normal-marine biotas into the Western Interior Seaway were therefore short lived, and primarily associated with sealevel highstand.

Organic-carbon analyses for the same interval (all data from Colorado and Kansas) demonstrate further restrictions to biotic migration during transgressive episodes which are associated with probable marine oxygen deficiencies. C_{org} curves show relatively high values (2 to 7% by weight) of organic carbon at several intervals during transgression of the Greenhorn and Niobrara cycles. These are commonly linked to episodes of reduced surface salinity determined isotopically; establishment of a subsaline cap on the surface of the Western Interior Seaway resulted in density stratification of the water-column, greatly reducing vertical exchange of oxygen from the surface to the bottom. With reduction or elimination of existing deep-water oxygen through metabolic processes and aerobic bacterial decay, the benthic and lower to middle parts of the water-column became stagnant, greatly restricting immigration and habitation by all but the most adaptive organisms. Reduced oxygen in the seaway is projected for intervals early in transgression, during middle transgression, near peak transgression, and during early regression of the eustatic cycles (Fig. 6). Oxygenation of the seaway to normal levels occurred mainly near peak transgression in association with normalization of surface salinity.

Finally, measurements of marine paleotemperatures can be interpreted from biological evidence and, broadly, from facies (e.g., pelagic carbonates vs. clay shales). These interpretations assume that Cretaceous organisms lived generally within the same thermal regime as their analogs in modern biogeographic provinces (see Hall, 1964). Based on these concepts, Kauffman (1973) provided lists of Cretaceous bivalve genera which characterized each major climatic zone; previously Sohl (1967, 1971) had done this for gastropods. Following these works, this study assumes that Cretaceous Tropical climatic zones were characterized by biogeographic units containing reefs or equivalent frameworks; and other taxa characteristic of modern Tropical carbonate platforms. Subtropical zones were characterized by similar taxa, but without formation of significant biotic frameworks. Warm Temperate environments contained diverse, large, thick-shelled molluscs, but lacked reef-builders and other taxa specialized for habitats of carbonate platforms. Faunas of the northern Gulf of Mexico are comparable. Mild Temperate faunas are interpreted as being moderately diverse assemblages of medium-sized, shelled invertebrates similar to those of the modern Virginian Province. Cool Temperate biotas are characterized by medium to small shelled organisms with moderate diversity. Specific taxa lists are being developed for these divisions.

Based on these comparisons, Cretaceous faunas from the interior of North America indicate that Cool Temperate to Warm Temperate climatic zones prevailed in the Western Interior seaway during most of its history. However, major northward migrations of Warm-Temperate and Subtropical biotas occurred near peak-transgression in all third-order and some fourth-order cyclothems.

Cretaceous Paleobiogeography of the Western Interior Seaway

Modern concepts of Cretaceous paleobiogeography for North America have only developed over the past two decades. Many early paleontologists recognized the unique aspect of faunas of the Western Interior Cretaceous, but none attempted to explain this in paleobiogeographic terms until Sohl (1967, 1971), Jeletzky (1971), Kauffman (1973), and Scott (1977) established the presence of two to three major paleobiogeographic divisions of the seaway, representing average expressions of broad climatic zones (Fig. 7). From north to south, these were: (a) a Cool Temperate biota derived from the northern Circum-Boreal Sea through southward invasion of the "middle" Cretaceous arm of the seaway (Fig. 3; Williams and Stelck, 1975, Text-figs. 2, 4); characteristic taxa of this biota are given by Jeletzky (1971; cephalopods), Sohl (1967, 1971; gastropods), and Kauffman (1973; bivalves). During average climatic conditions for the Western Interior (Temperate Zone-dominated) the northern paleobiogeographic division extended from the Cretaceous Circum-Boreal Sea to the southern borders of Montana, Idaho, and North Dakota (Fig. 7). (b) a Mild Temperate biota found between northern Wyoming – South Dakota, and north-central Utah, northern Colorado, and Kansas (Fig. 7); this division also encompasses most of a broad zone of mixing (ecotone) of northern Cool Temperate and southern Warm Temperate biotas (see Sohl, 1967, Fig. 7). The unique elements of this subprovince are mainly rapidly evolving endemic taxa; high levels of endemism were possibly caused by widespread ecological distruption of northern and southern ecological units (communities) in the broad paleobiogeographic ecotone. (c) a Warm Temperate southern biota derived from the Gulf and Atlantic Coast Subprovince (Kauffman, 1973) during northward invasion of the southern arm of the Western Interior Seaway (Fig. 3). This biota normally occurred between southeastern Utah, northeastern Nevada, northern Arizona, New Mexico, northern Texas, central to southern Kansas, and northwestern Oklahoma (Fig. 7). Typical biotas are described by Scott (1970, 1977).

Paleobiographic concepts and nomenclature have been applied variably to these divisions. Most early authors considered

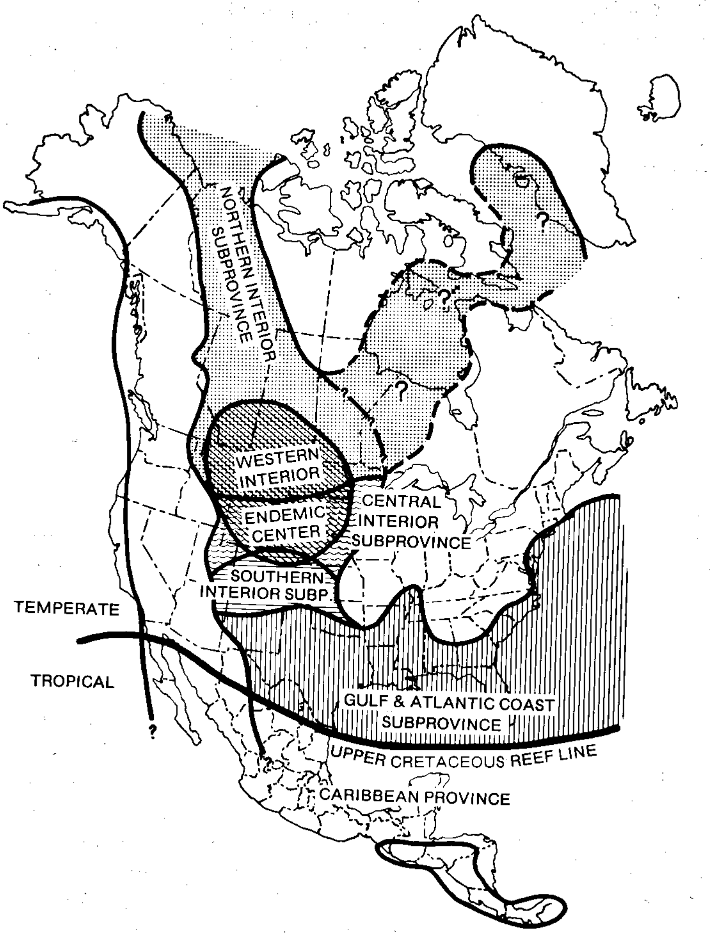

Figure 7. Generalized map of the Western Interior Cretaceous Seaway of North America, showing average distribution of paleobiogeographic units (Subprovinces, Provinces) during early to middle transgression and middle to late regression associated with all third-order tectonoeustatic cycles. Map also shows average extent of paleobiogeographic ecotone (endemic center), within which most rapid evolution took place. Subprovinces and provinces defined on percent molluscan endemism (10 to 25% and 25 to 50%, respectively). From north to south, subprovinces reflect Cool Temperate, Mild Temperate, Warm Temperate, and Subtropical climatic zones, as defined in modern American coastal settings by Hall (1964) and others.

the entire Western Interior Cretaceous biota as all or part of the "North American Province". Jeletzky (1971) recognized "northern and southern divisions" of this biota and Sohl (1971) recognized "northern" and "southern" divisions of the "Western Interior Region". Kauffman (1973), based on measures of endemism for Cretaceous bivalves and comparison of these values to modern biogeographic concepts, determined that bivalve endemism within the Western Interior was only 5 to 10% and not deserving of provincial rank. Kauffman thus named a "Western Interior Endemic Center", extending from the central into the northern part of the basin, and recognized the southern interior biota as a "northern arm of the Gulf and Atlantic Coast Subprovince"; the North American Province was expanded to include the Atlantic and Gulf Coast biota, as well as the Western Interior biota. Subsequent work has demonstrated that the bivalves are biogeographically somewhat atypical of this seaway, and that Western Interior endemism is higher for other groups of invertebrates. This allows a more refined paleobiogeographic division of the seaway. Scott (1977) recognized a Southern Western Interior Province for Warm Temperate biotas of Kansas, Oklahoma, New Mexico, northeastern Arizona, and northern Texas (Fig. 7); calculations of endemism percentages suggest that this division is of subprovincial rank, utilizing the scheme of Kauffman (1973).

In this paper and in Coates *et al.* (1984), a new scheme of paleobiogeographic division is employed, one which is consistent with modern biogeographic concepts and their ancient equivalents (Kauffman, 1973). Figure 7 shows these divisions as averaged for the Western Interior Seaway during most of its marine history but exclusive of peak transgression. Following Jeletzky (1971) with modification, the northern Cool Temperate biota of the seaway is termed the Northern Interior Subprovince; the Mild Temperate biota of Colorado, northern New Mexico, and Kansas is termed the Central Interior Subprovince (new name); and following Scott (1977), the southern Warm Temperate biota is called the Southern Interior Subprovince. All subprovinces, along with the Gulf and Atlantic Coast Subprovince of Kauffman (1973), are placed within the North American Province of Kauffman (1973). Percentages of endemism for genera and species groups range between 10 and 25 per cent for all subprovinces recognized above.

A modified use "North American Endemic Center" (Kauffman, 1973) is applied to the main zone of paleobiogeographic overlap (ecotone) between the Cool Temperate Northern Interior biotas, and the Warm Temperate Southern Interior biotas (Fig. 7; Sohl, 1967, Fig. 7). This zone incorporates most areas of endemism within the Interior Seaway and spans the northernmost edge of the Southern Interior Subprovince, most of the Central Interior Subprovince, and the southern third of the Northern Interior Subprovince. Endemism is particularly evident in ammonite groups like the Gastroplitidae (e.g., Reeside and Cobban, 1960), Scaphitidae (e.g., Cobban, 1951a, 1969), and Baculitidae (e.g., Cobban, 1951b, 1958, 1962a, 1962b); and among bivalves of the Inoceramidae (e.g., the Albian-Cenomanian *"Inoceramus" dunveganensis, "I." athabaskensis*, and *"I." moberliensis* lineages; Kauffman, 1977c). In utilizing the term "endemic center" in this evolutionary sense, I remove it from the hierarchy of paleobiogeographic classification of Kauffman (1973).

South of the Western Interior Seaway and connected to it through a somewhat narrow aperture (Fig. 7) lay the Cretaceous Gulf of Mexico and Caribbean Sea, at the northern edge of, and within the Tropical Tethyan Realm, respectively (Fig. 7; Kauffman, 1973). During times of normal distribution of paleobiogeographic units in the Western Interior Seaway (Fig. 7), the Gulf and Atlantic Coast Subprovince contained a mixture of southern Warm Temperate and Subtropical taxa; the biota had great diversity, abundance of medium to large-size, shelly species, and many reef and carbonate platform-associated taxa but without the formation of large organic frameworks. Detailed analysis of this region will probably allow eventual subdivision of the Gulf Coast biotas into a northern group dominated by Warm Temperate organisms related to those of the Southern Interior Subprovince, and a southern group dominated by Subtropical organisms related more to those of Tethys.

The Tethyan biota is represented by the Caribbean Province and dominated by Tropical mollusc, echinoderm, and larger foraminifer assemblages, as well as by reef-like buildups of corals, calcareous algae, rudistid bivalves, and associated taxa.

An understanding of these paleobiographic divisions is necessary for the interpretation of dynamic paleobiogeographic changes in the Western Interior. Episodically, these changes involved rapid immigration and emmigration of Subtropical and Tropical taxa through the southern half of the Seaway. Figure 7 is an average expression of paleobiogeographic distribution patterns within the Western Interior Seaway, not a static situation. It provides, however, a useful base for a study of paleobiogeographic dynamics within the basin.

Dynamic Changes in Paleobiogeographic Units of the Western Interior Seaway

The average Upper Cretaceous paleobiogeographic distribution of marine biotas, reflecting climatic zones in North America (Fig. 7) has been determined by careful analyses of the distribution of many marine groups. This has led to identification of characteristic taxa for each subprovince which allow it to be mapped in time and space, and to the definition of broad ecotonal boundaries (e.g., Sohl, 1967) between subprovinces. These boundaries can be mapped through time in the same way that Gill and Cobban (1973) have mapped Cretaceous strand lines. With these data in hand, it is now possible to examine the hypothesis that paleobiogeographic units like those of the Western Interior epicontinental seaway are dynamic – shifting continuously in response to changes in tectonoeustacy, paleoceanography and regional geology.

The distributions of North American paleobiogeographic units and their boundaries have been plotted from regional biotic data throughout the 34 Ma Albian-Maastrichtian history of the Western Interior Seaway. Data have then been lumped into substage groupings, averaging 2.0 Ma in duration in order to map and compare the paleobiological data through the paleobiogeographic history of the Western Interior Cretaceous Seaway (Figs. 8-13). Paleobiogeographic plots at this resolution reveal dynamic shifts over short time intervals in the North American subprovinces, and especially in the distribution of the Southern Interior and Gulf and Atlantic Coast Subprovinces during maximum transgression and eustatic highstand.

In summary, prior to long-term connection of the southern and northern arms of the seaway in the earliest Cenomanian (Fig. 3; Williams and Stelck, 1975), Cool Temperate biotas, which occupied the northern arm, were only slightly differentiated from those of the Circum-Boreal Seaway, where they had originated. Only at maximum Late Albian penetration into central Colorado (Fig. 3; Williams and Stelck, 1975, Text-Fig. 4) did significant endemism develop within the northern arm among gastroplitid ammonites and inoceramid bivalves (Reeside and Cobban, 1960, Kennedy and Cobban, 1976). Similarly, during the Albian, the more restricted southern arm of the seaway (Fig. 3; Williams and Stelck, 1975, Text-Figs. 2, 4) contained Warm Temperate to Subtropical biotas which were less diverse but very similar to those of the Gulf and Atlantic Subprovince. The two biotas overlapped briefly during a short middle Late Albian connection of these seaways. Without significant endemism in either arm of the seaway, distinct paleobiogeographic units could not be defined and these two biotas are grouped with the Circum-Boreal and Gulf and Atlantic Subprovinces, respectively, in plotting Albian paleobiogeography. Further, Kauffman noted (1973, Fig. 4) that rates of pre-Cenomanian seafloor spreading and opening of the Atlantic were not sufficient to achieve widespread genetic isolation of the North American biota from that of Western Europe; distances across the Atlantic were still within reach of westward larval dispersal for many taxa. As a consequence, North American endemism in general was restricted, and paleobiogeographic differentiation occurred at very low levels during the Albian. Endemism at subprovincial levels did not occur in the Gulf and Atlantic Coast or the Western Interior until the Cenomanian.

(2) Following Early Cenomanian connection of the northern and southern arms of the Western Interior Seaway, and due to extensive genetic isolation among North American marine biotas as the Atlantic Ocean basin opened to distances which exceeded larval dispersal ranges for many benthic taxa from European marine ecosystems – discrete North Temperate and Tethyan Realm provinces and subprovinces became rapidly differentiated in North America (Kauffman, 1973, Fig. 4). Figure 7 defines the average expression of these new paleobiogeographic units during Cenomanian-Maastrichtian time, a pattern that was generally persistent, with boundary migrations rarely exceeding 200 miles (320 km), through most of the transgressive and regressive phases of each eustatic cycle over 35 Ma. This relative biogeographic stability was, in part, probably due to the ecological restriction of the biota during these invervals; diversity was relatively low due to subnormal surface salinities and less than normal oxygen in the middle and lower water column. Ecological generalists, many with cosmopolitan and intercontinental distribution, and low-diversity, endemic biotas occupied these stressed environments, making precise tracing of paleobiogeographic fluctuations difficult; these physically accommodated ecosystems, dominated by eurytopic generalists, would be expected to show low levels of paleobiogeographic response to broadly and slowly changing environments of long-term transgression and regression.

(3) Detailed paleobiogeographic mapping does reveal exceptionally rapid, broad shifts in North American subprovinces for each cyclothem just prior to, during, and just after peak rise of sealevel and epicontinental transgression. These are especially evident during the extensive Early Turonian and Coniacian through Santonian transgressions (eustatic highstands). In each cycle the rate and magnitude of paleobiogeographic change is correlative with the relative magnitude and duration of the third-order eustatic fluctuation. These abrupt biogeographic changes are fully predictable from our basin models utilizing tectonic, sedimentologic, biologic and geochemical evidence.

SUMMARY

Several important geologic and oceanographic events converged during peak rise of sealevel of create conditions favorable to widespread rapid shifts in the distribution of paleobiogeographic units. Maximum elevation of sealevel accompanied maximum subsidence of the Western Interior Basin due to tectonic and sediment loading, modified probably by shallow plate subduction. Subsidence outstripped sedimentation, so that the deepest water of the basin history was developed during peak transgression and, with it, maximum opportunities for development of strong, multilayered current systems down the western and central part of the basin. These conditions favored immigration of biotas from surrounding ecosystems through mobility of adult plankton and nekton, or by dispersal of the planktonic larvae of benthic organisms in the upper water column. Both rise of sealevel and deepening of the basin were progressive however, so that rapid immigration of taxa near peak-rise of sealevel is not predictable from these factors alone. Rapid biogeographic changes are predictable, however, from geochemical and biological data which suggest that brackish, oxygen-deficient waters within Cool to Warm Temperate climatic belts dominated the seaway during much of the transgressive and regressive history of the cyclothems. These conditions favored immigration of more generalized northern faunal elements into the basin; this was countered, however, by broad warming associated with increasing maritime climates during transgression. Deleterious chemical environments of the seaway further discouraged widespread immigration of normal-marine taxa from northern and southern biogeographic units. Marine larvae, especially, are very sensitive to abnormal water-chemistry and temperature (Kauffman, 1975; Scheltema, 1977). Further, the possible development of at least a partial sill at the constricted southern end of the seaway, holding back major warm currents during sealevel rise until some depth-threshold was reached, cannot be ruled out as a contributing factor to retention of a semi-stable Temperate biogeography during most of transgressive history in the seaway (Fig. 7).

However, sedimentologic, geochemical, and paleobiologic data clearly show rapid, major changes in the watermass of the Western Interior Seaway within 1 to 2 Ma of peak-eustatic rise during the middle Late Albian, Late Cenomanian to Early Turonian, during transgressive pulses of the Coniacian-Santonian, during the late Early Campanian, and during the middle Late Campanian. These changes are variably characterized by onset of pelagic (foraminiferal-coccolith) carbonate deposition in dominantly non-calcareous sequences; by isotopic changes indicating normalization of salinity and extensive oxygenation throughout the water column; by episodic decrease in organic-carbon content of sediments associated with periods of benthic oxygenation; by physical evidence of current-mixing in deep-water sediments, and by the migration and introduction of numerous taxa characteristic of the Gulf and Atlantic Coast Subprovince (Warm Temperate to Subtropical) and, to a lesser degree, of the Tropical Caribbean Province. These rapid physical and chemical shifts are indicated in data presented on Figures 4-6. The extent of northward migrations of warm water taxa from the Gulf and Caribbean biotas are shown on Figures 8-13, with Figure 7 being the average expression of paleobiogeographic distributions between sealevel peaks. Radiometric dating of strata containing evidence for large, rapid shifts in paleobiogeographic distributions indicate that these changes took place in less than a million years, usually within a half million years. Events associated with biogeographic migrations depicted in Figures 8-13 during eposides of peak-rise of sealevel in the Greenhorn and Niobrara Cycles is drawn from the more extensive work of Coates, Kauffman, and Sohl (in press).

The Middle Late Albian Incursion. The first trough connection between the southern and northern arms of the Western Interior seaway occurred in the middle Late Albian (zones of *"Inoceramus" comancheanus*; *"I." bellvuensis*: Kauffman, 1975; Kauffman *et al.*, 1976) with the initial junction in south-central Colorado. This connection followed a long period of progressive incursion of the northern and southern arms of the seaway (Aptian-Middle Albian; 15 Ma); during this interval Cool Temperate Circum-Boreal biotas migrated as far south as northern Colorado, and Warm Temperate to Subtropical biotas migrated as far north as southern Colorado, Oklahoma, and central Kansas. Excepting for important development of endemic ammonites and bivalves in the distal (southern) reaches of the northern arm the Cool Temperate biota was a diminished version of the Circum-Boreal Canadian-Alaska biota. The distal reaches of the southern arm of the seaway had its strongest affiliations to the Warm Temperate-Subtropical biota of the Texas Gulf Coast, and only low levels of endemism.

In contrast to the paucity of southern warm water elements that immigrated into the Western Interior seaway during Aptian-Middle Albian time, at the southern aperture of the seaway this interval was marked by significant paleobiogeographic change. Warm Temperate Aptian biotas were replaced first by Subtropical assemblages and ultimately by Tropical reef-associated biotas in northern Mexico, central Texas, southern New Mexico, and southern Arizona during the Albian. Stoyanow (1949) documented cosmopolitan and Warm Temperate biotas in southern Arizona in the Early Aptian (*Deshaysites* Assemblage), Subtropical marginal Tethyan forms in the Middle and Upper Aptian (*Kazanskyella* through *Hypacanthoplites* assemblages), and fully Tropical Tethyan biotas, including rudist-coral reefs during the Albian (Scott and Brenckle, 1977). This sequence depicts a significant northward migration of the Temperate-Subtropical and Subtropical-Tropical biogeographic boundaries across Mexico and Texas during the Aptian-Albian, associated with rising sealevel. Compare the Albian reef line (Fig. 8) with the average Upper Cretaceous reef line (Fig. 7) 650 to 800 km to the south. Maximum northward Lower Cretaceous migration of these boundaries culminated in the development of rudist-dominated frameworks throughout central Texas by the early Middle Albian (e.g., Perkins, 1974, Fig. 2) and their proliferation into the Upper Albian of Texas, southern Arizona, and southern New Mexico. Young (1972) also noted episodic northward migrations of "cosmopolitan" Tethyan ammonites into central Texas during the Albian, and related this to breaching of the "barrier reef" (bank) at the southern edge of the Comanche shelf. Despite progressive northward migration of Tethyan and Marginal Tethyan biotas into Texas during the Aptian-Albian, none entered the southern end of the Western Interior basin before the Late Albian.

By the time warm Tethyan waters first overstepped the res-

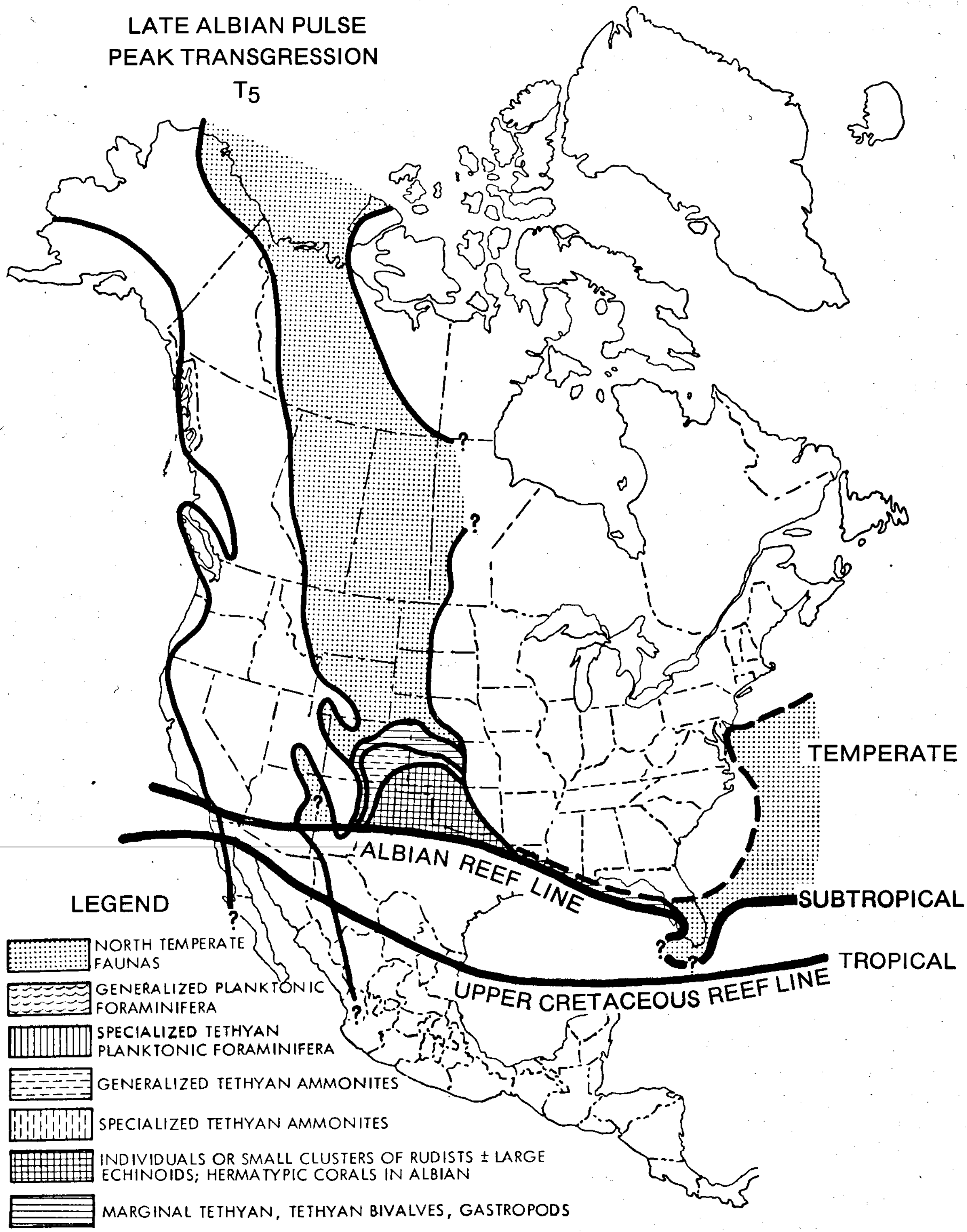

Figure 8. Generalized map of the Western Interior Cretaceous Seaway of North America during peak Late Albian transgression associated with the Kiowa-Skull Creek Eustatic Cycle. Map shows distribution of various Subtropical organisms (patterns keyed to lower left of diagram) defining northward shift of Temperate-Subtropical paleobiogeographic units during brief incursion of warm normal marine waters into the seaway at eustatic high-stand. Note in particular brief northward shift of Albian Tropical reef line from normal Upper Cretaceous position (heavy dark line). **Compare** with more normal **paleobiogeographic** distributions in **Figure** 7.

tricted southern aperture of the Western Interior Seaway, therefore, a major buildup of Tethyan biotas had already occurred just to the south, and the Tethyan reef boundary had attained its maximum northerly position for the entire Cretaceous (Fig. 8). The stage was thus set for a rapid northward Tethyan incursion into the Western Interior seaway once the Late Albian eustatic rise widened and then breached the restricted southern aperture of the basin. Early Late Albian immigration of Subtropical biotas mainly from the southeast took less than a half million years to reach southern Kansas, northwestern Oklahoma, and New Mexico.

Twenhofel (1924) and Scott (1970, 1977) documented the following sequence of events. (a) Rapid marine transgression into the southern part of the Western Interior Basin during the early Late Albian; marginal Tethyan influence was initially strong. The "Champion Draw Bed" (Cragin, 1895; Twenhofel, 1924, Scott, 1970, 1977: upper *Venezoliceras kiowanum* Zone) of southern Kansas contains the highest diversity (36 species) and the strongest marginal-Tethyan faunal affinities (60 to 65% similarity with the Texas Gulf Coast) for the entire Late Albian transgression. The fauna includes small isolated, hermatypic coral colonies *(Astrocoenia)* but no reefs. Other Subtropical elements include *Venezoliceras*, bivalves like *Texagryphaea, Ceratostreon*, large *Trachycardium*, and *Cucullaea*, trochid and granulated turritellid gastropods, and the Tethyan echinoid *Salenia*. There is little endemism in this biota. (b) Continued middle Late Albian transgression (zone of *Adkinsites bravoensis*) extended the sea into southern Colorado and central Kansas. Partial closing of the southeastern aperture of the seaway by a major deltaic complex, shifted the principal source of warm southern waters and biotas to the Chihuahua Trough. Marginal-Tethyan influence remained high, involving many of the same molluscan genera that characterized the Champion Draw biota, additional Subtropical bivalves like *Roudaria* and *Neithea fredericksburgenesis* (Cragin), generalized planktonic foraminifera, and an expanded Tethyan ammonite assemblage including *Adkinsites, Venezoliceras*, and *Manuaniceras*. But collectively, the middle Late Albian fauna had less similarity (50%) to the Marginal Tethyan faunas of Texas than before, and lacked hermatypic corals; decrease in Tethyan influence was coincident with increasing percentages of normally Warm Temperate taxa, and significantly higher levels of endemism, marking origination of the Southern Interior Subprovince (Scott, 1977). Marginal Tethyan biotas extended further north during the middle Late Albian than earlier in the transgression. (c) During the latter part of the middle Late Albian (*"Inoceramus" comancheanus* Zone) the two arms of the Western Interior Seaway first joined in central Colorado. Mixing and competition among the Marginal Tethyan – Warm Temperate southern biota and the Cool Temperate northern biota ensued. An initially sharp biogeographic boundary gave way to a broad zone of faunal mixing (ecotone) between Colorado and Texas. Marginal Tethyan bivalves like *Texigryphaea* and large *Trachycardium* reached south-central Colorado while northern inoceramid lineages reached north Texas. Overall Tethyan influence declined sharply and diversity decreased. Strong eastern (Kansas: 24%) and western (New Mexico-Colorado: 9%) endemic centers (Scott, 1977, p. 167) developed. The Marginal Tethyan – Temperate boundary retreated southward into New Mexico during the Late Albian, leaving behind isolated Subtropical faunal elements. (d) During the late Late Albian (*"Inoceramus" bellvuensis* Zone) the Western Interior seaway attained its maximum Lower Cretaceous development at peak-transgression; this was closely followed by basinal filling, shoaling, and rapid Late Albian regression. Whereas a few Marginal Tethyan molluscs reached their maximum penetration into north-central Colorado at this time (Fig. 8), the fauna of the southern seaway was predominantly Warm Temperate. The Warm Temperate – Marginal Tethyan boundary retreated into Texas, beyond the aperture of the seaway, and the Cretaceous reef-line retreated into northern Mexico (Fig. 7 *vs.* Fig. 8) during the Late Albian regression (T_6; Fig. 4). The Late Albian incursion of Subtropical biotas into the Western Interior lasted approximately 0.5 to 1.0 Ma (Fig. 4), with maximum northward migration of the Tropical Caribbean Province-Subtropical Atlantic Coast-Southern Interior Subprovince boundary of about 1100 km.

The Late Cenomanian-Early Turonian Incursion. One of the most dramatic incursions of Tethyan and Marginal Tethyan biotas into the Western Interior Seaway occurred near and at the peak of the great Cenomanian Transgression (T_6; Fig. 4; Hancock and Kauffman, 1979), in a 2.5 Ma interval spanning latest Cenomanian and Early Turonian time. (a) This transgression began during the latest Albian (*Neogastroplites* zones) with eustatic rise, re-advance of the northern (Cool to Mild Temperate) arm of the seaway, and buildup of Subtropical Tethyan influence northward across the Texas Comanche Shelf without breaching the southern aperture of the Interior Seaway. By latest Albian, the northern arm of the seaway reached southern Colorado (Fig. 3), bearing a discrete Northern Interior Subprovince biota rich in endemic ammonite and bivalve species. Equivalent strata in Texas record northward transgression across the Comanche Shelf, and a change from cosmopolitan molluscs of the *Mortoniceras wintoni* assemblage to Tropical-Subtropical Tethyan assemblages (including many endemics) of the *Drakeoceras gabrielense* Zone (Young, 1972); extensive platform carbonates developed concurrently.

(b) During the Early Cenomanian the Western Interior Temperate biota was still largely isolated from that of Gulf Coast shelf seas by a shallow clastic sedimentary sill (Woodbine Formation and equivalents) across the southern aperture. The Early Cenomanian biota of the Western Interior was predominantly Cool to Mild Temperate, with high endemism among the dominant inoceramid bivalves and ammonites. The Northern and Central Interior Subprovinces were broadly differentiated, with a diffuse ecotonal boundary. In Texas, however, Young (1972) documented increasing Early Cenomanian endemism and Tethyan influence among ammonite faunas of the Comanche Shelf. Thus, Early Cenomanian eustatic rise coincidently caused buildup of Tropical to Subtropical Tethyan biotas in the Gulf Coast and initiated widespread invasion of the Interior Seaway, mainly from the north. But the restricted southern aperture of the basin remained as an effective barrier to northward immigration of warm-water taxa, as did the slightly brackish, oxygen-restricted chemistry of the interior seaway at this time.

(c) By Middle Cenomanian time the barrier at the southern aperture of the Western Interior basin was breached with continued eustatic rise. A broad zone of intermixing of northern and southern Temperate biotas was quickly established in the southern one-third of the Western Interior and Texas (Stephenson, 1952); rare Subtropical elements (rudists, specialized planktonic foraminifera, etc.), reached southern Colorado. Gradual northward expansion of Warm Temperate and cosmopolitan taxa and short-lived incursions of generalized, eurythermal, planktonic foraminiferans (Eicher, 1977, Fig. 1) suggest increasing water temperatures and slow northward expansion of the Southern Interior Subprovince. Still, Temperate zone biotas predominated throughout the seaway during the Middle Cenomanian.

(d) Warm-water cosmopolitan and marginal-Tethyan (Subtropical) taxa first immigrated into the southern half of the Western Interior Seaway during the Late Cenomanian, beginning with a few specialized (stenothermal), planktonic foraminiferans and calcareous nannoplankton, which then diversified gradually through the substage forming widespread pelagic carbonates (Eicher, 1977, fig. 1; Kauffman, 1984). The gradual buildup of Tethyan influence in the southern part of the Western Interior seaway was abruptly altered through a remarkable series of environmental and biological events during the Late Cenomanian (*Dunveganoceras pondi, D. albertense*, and *Sciponoceras gracile* zones) and Early Turonian (Kauffman and Scholle, 1977; Scholle and Kauffman, 1977; Kauffman, 1984). These gave rise to an extensive, short-term incursion of Tethyan waters which carried the Warm Temperate-Subtropical paleobiogeographic boundary nearly 1300 miles (2080 km) to the north (Fig. 9) and back again in 2.5 to 3 Ma, as follows.

(e) Near peak-transgression (lower *S. gracile* Zone) stable isotope, sedimentologic, and biologic data indicate initiation of a sharp rise in water temperature and salinity levels throughout the central and southern part of the seaway. This marks abrupt flooding of Gulf and Caribbean watermasses into the Western Interior as a result of rapid eustatic rise and/or sudden breaching of barriers in the southern aperture of the seaway in less than 0.5 Ma. This generally correlates with a marked Late Cenomanian decline in the effectiveness of the Stuart City "reef" as a barrier to northward ammonite migration (Young, 1972). (f) This temperature/salinity change produced a dramatic increase in marine diversity throughout the southern half of the Western Interior basin. Koch (1978, 1980) reported 170 macrofaunal taxa in the *S. gracile* Zone, a six-fold increase over diversity recorded from immediately underlying strata (Kauffman, 1984). Eicher (1977, Fig. 1) recorded an increase from 0 to 30 benthic calcareous foraminiferal species, and from 10 to 15 planktonic species, across this marked environmental boundary. This rapid increase in diversity resulted from: increased rates of evolution due to temperature and salinity stress (Kauffman, 1978); widespread mixing of southern and northern biotas leading to temporary niche partitioning and exploitation of new habitats; widespread endemism among Warm Temperate elements; and immigration and ecological accommodation of many cosmopolitan and some marginal Tethyan taxa, including warm-water radiolitid rudists, the large echinoid *Holaster*, Subtropical ammonites *(Desmoceras, Pseudouhligella, Anisoceras)*, large *Trachycardium* and gastropods like *Nerinea* and *Cassiope* (Sohl, 1967, 1971). The now diffuse Subtropical (Gulf and Atlantic Coast Subprovince) – Warm Temperate (Southern Interior Subprovince) boundary migrated northward into New Mexico and southern Utah, and the Warm Temperate – Mild Temperate (Central Interior Subprovince) boundary as far north as central Montana and southern Alberta, by the end of the Cenomanian.

(g) A major extinction event occurred just below and at the Cenomanian – Turonian boundary (Kauffman, 1984), largely involving the loss of endemic, Warm Temperate and cosmopolitan elements of the *Sciponoceras gracile* Zone macrofauna (Koch, 1978) and the calcareous benthic microfauna (Eicher, 1977, Fig. 1). This was associated with a significant shift in oxygen isotope values indicating a major drop in salinity just prior to peak-transgression (Pratt, 1983, and pers. commun.) and severe stratification of the water-column leading to an oxygen crisis in the seaway, reflecting a global anoxic event (The Bonarelli Event). Sediments immediately overlying the extinction level intermittently contain high levels of C_{org} and only rare, eurytopic latest Cenomanian molluscs. (h) Reoxygenation of the seaway accompanying still rising temperature and salinity levels within the first 0.5 Ma of the Turonian produced abrupt northward migration of the Subtropical biota. The Subtropical Gulf and Atlantic Coast Subprovince – Southern Interior Subprovince (Warm Temperate) boundary reached into southern Canada, Montana, and North Dakota as defined by the northernmost extension of keeled, planktonic foraminiferans and relatively diverse, marginal-Tethyan macrofaunas, predominantly molluscs like *Cassiope* (Sohl, 1967, 1971), radiolitid rudists, *Holaster* (echinoid) and varied Tethyan ammonites *(Fagesia, Vascoceras, Ampakabites, Choffaticeras*, and *Nigericeras)*. This maximum incursion of Tethyan biotas during the Middle Cretaceous (Fig. 9) coincided with peak transgression (T_6; Fig. 4), peak eustatic rise, and maximum marine warming (zones of *Watinoceras coloradoense* and *Mammites nodosoides*). (i) This Subtropical biota diversified during the middle and late Early Turonian (one Ma). Kauffman (1984) recorded a rapid change from 2 to 13 to 28 molluscan taxa, and Eicher (1977, Fig. 1) recorded an increase from 15 to 20 planktonic foraminifera species through the lower three inoceramid zones of the Early Turonian in Colorado. Warm to Mild Temperate biotas spread well up into central Alberta with correlative retreat of the Northern Interior Subprovince; (j) Subtropical immigrants in the Western Interior biota gradually decreased in numbers, diversity, and biogeographic range during the latest Early and early Middle Turonian (*Mytiloides labiatus* s.s. Zone; *Collignoniceras woollgari* Zone), 2.5 to 3 Ma after their abrupt immigration. This decline was associated with initial eustatic fall, early regression (R_6; Fig. 4), and lowering of epicontinental marine temperatures and salinity in the seaway. Kauffman (1984) recorded an 86 per cent decrease in macrofossil diversity and Eicher (1977) documented a similar decline in planktonic foraminiferal diversity in the basinal center during the early Middle Turonian. The Subtropical – Warm Temperate paleobiogeographic boundary retreated southward nearly 1,000 miles (1,600 km) during this 1.5 Ma period, and Cool and Mild Temperate biotas became re-established to the

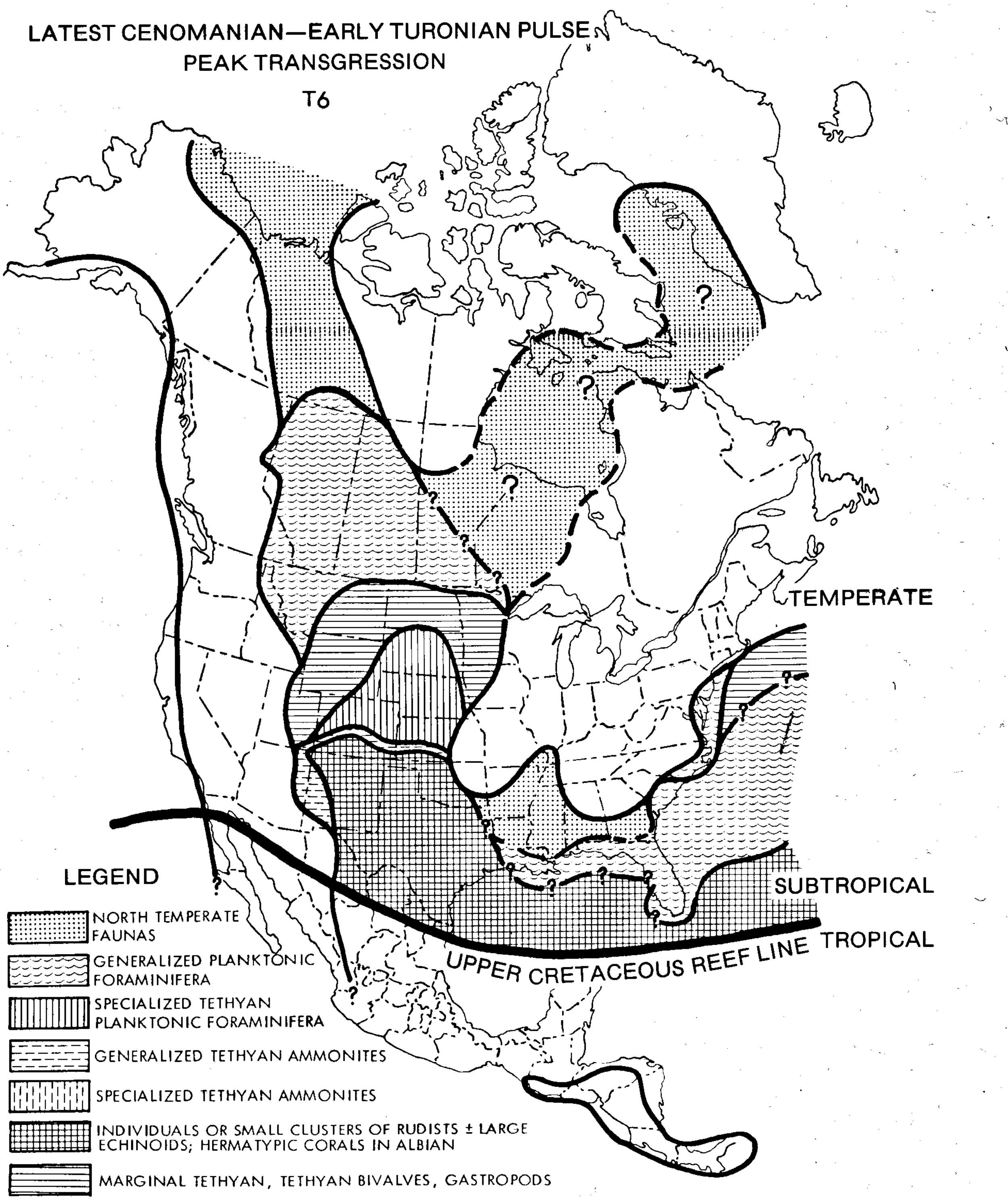

Figure 9. Generalized map of Western Interior Cretaceous Seaway of North America during peak Early Turonian transgression associated with the Greenhorn Eustatic Cycle. Map shows distribution of various Subtropical organisms (patterns keyed to lower left of diagram), defining extensive, short-term, northward migration of Warm Temperate and Subtropical paleobiogeographic units during rapid incursion of warm, normal marine waters into the seaway at eustatic highstand. Compare with more normal paleobiogeographic distributions in Figure 7.

south, attaining their "normal" biogeographic position (Fig. 7) by the Middle Turonian.

The Coniacian-Santonian Tethyan Incursion. The second-most extensive incursion of Subtropical biotas into the Western Interior Seaway occurred during the Early Coniacian to Late Santonian Niobrara eustatic cycle (Fig. 10), a time of sealevel highstand and global warming (Fig. 4). Four separate incursions were each linked to a small fourth-order transgressive pulse (T_{7a}, T_{7b}, T_{7c}, T_{7d}; Fig. 4); minor regressions separate these pulses. The Lower Coniacian (T_{7a}) and Middle Santonian (T_{7c}) transgressions were significantly more extensive than the others. The Coniacian-Santonian eustatic cycle consists in the central and eastern part of the seaway of abundant pelagic chalks or limestones bearing numerous Subtropical biotic elements during transgressive peaks; these alternate with calcareous shale or finely laminated, pelagic marls yielding a cosmopolitan warm-water biota during regression. The entire pelagic carbonate interval in the southern and central part of the basin contains diverse planktonic foraminiferans, including keeled stenothermal forms and calcareous nannoplankton; Kent (1967) provides partial documentation. The following sequence of events characterize this incursion, and are abstracted from Coates *et al.* (1984).

(a) During rapid (0.5 Ma) initial eustatic rise of sealevel associated with the Niobrara marine cycle early and middle transgressive sediments of the Western Interior and northern Gulf Coast consisted of sands, calcarenites, and clays lacking significant pelagic carbonate and bearing Temperate endemic and cosmopolitan biotas of moderately low diversity. The basin was somewhat subsaline and oxygen-restricted throughout.

(b) During the latest Turonian (zone of *Prionocyclus quadratus*) and earliest Coniacian (middle T_{7a} transgression; Fig. 4) pelagic carbonates containing low diversity assemblages of Warm Temperate to Subtropical microplankton (Kent, 1967) became abruptly widespread (<250 Ka) in the central and southern part of the seaway. These, and moderately diverse warm-water macrofaunas, document northward expansion of the Southern Interior Subprovince to at least southern Wyoming. Scholle and Kauffman (1977) noted a significant change in $\delta^{18}O$ and $\delta^{13}C$ isotopic values associated with the initial spread of these uppermost Turonian – lowest Coniacian carbonates suggesting an abrupt increase in water temperature and/or normalization of salinity. Coincidently, abundance and diversity of warm-water biotas increased sharply. Macrofaunal composition changed rapidly from wholly Warm Temperate to predominantly warm-water cosmopolitan assemblages, but initially lacked Subtropical elements. The similarities between this diversification event and the one immediately following the Late Cenomanian change in temperature/salinity values are striking.

(c) A major extinction event followed, abruptly eliminating most Warm Temperate and many cosmopolitan marine taxa and marking the Turonian – Coniacian boundary (basal Niobrara Formation and equivalents). Isotopic and biologic data indicate stable temperatures and near-normal salinity levels across the boundary. But Lower Coniacian limestones enriched in pyrite, marcasite, and limonite and organic-rich marls contain only sparse eurytopic molluscs and foraminifers (Kent, 1967; Kauffman, 1984) recording widespread, short-term (0.1 Ma) oxygen depletion in the Western Interior Basin, one which has a global imprint. This anoxic event, coupled with ecological stress imposed by relatively rapid temperature/salinity increase during the latest Turonian and earliest Coniacian was probably responsible for the extinction event.

(d) Isotopic and biologic data (Scholle and Kauffman, 1977) suggest a second, smaller, increase in temperature and/or salinity within the Western Interior seaway at the first peak of Niobrara transgression (T_{7a}). This coincides with abrupt appearance (<0.25 Ma) and diversification of the Lower Coniacian biota (*Inoceramus erectus* and *I. deformis* zones), including southern Interior Warm Temperate groups, generalized warm-water cosmopolitan stocks, and Subtropical biotas from the Tethyan margin (e.g. the rudist *Durania* in small clusters, Tethyan ammonites like *Forresteria, Barroisiceras* and *Peroniceras*, keeled planktonic foraminifers to Wyoming and South Dakota, and generalized planktonics into southern Canada; Fig. 10). This marks rapid northward migration of the diffuse Gulf and Atlantic Coast Subprovince – Southern Interior Subprovince boundary approximately 600 miles (1,000 km) to central Wyoming and South Dakota (Fig. 10). Simultaneously, the Southern Interior – Central Interior Subprovince boundary migrated nearly 700 miles (1,100 km) northward into southern Canada. No core-Tethyan faunas entered the Western Interior Basin.

(e) Subsequent fourth-order fluctuations in sealevel during Coniacian-Santonian time produced small-scale changes in the distributions of these Subtropical and Warm Temperate Western Interior biotas. Gradual decline in marginal-Tethyan biotic influence and slow southward retreat of the Subtropical – Warm Temperate boundary began in the late Early Coiacian and culminated in the Middle Coniacian, coincident with a fourth-order regression (R_{7a}) and a small but abrupt decline in salinity and water temperature. Concurrently, molluscan and calcareous microplanktonic diversity decreased in the northern and central parts of the basin (Kent, 1967; Kauffman, 1984); cosmopolitan ecological generalists replaced specialized Subtropical elements of the biota during the late Early Coniacian. By Middle Coniacian time (lower *Scaphites ventricosus* Zone) the Subtropical-Warm Temperate biogeographic boundary retreated approximately 400 miles (650 km) south to Colorado.

(f) A second Coniacian-Santonian incursion of warm-water biotas occurred during the late Middle to Late Coniacian fourth-order transgressive peak (T_{7b}; Zone of *Scaphites ventricosus* and *Magadiceramus subquadratus*). It is represented near the basinal center as far north as Wyoming by widespread, pelagic chalks and limestones containing diverse calcareous foraminifer and nannoplankton with Tethyan affinities (Kent, 1967). Sparse isotopic data across this limestone suggest a small increase in temperature and/or salinity. This interpretation is confirmed by the reappearance of a Marginal Tethyan macrofauna up to northern Colorado and southern Wyoming, including sparse radiolitid rudists (*Durania*) and the ammonite *Peroniceras.* Northward re-advance of the Subtropical Gulf Coast – Warm Temperate, Southern Interior paleobiogeographic

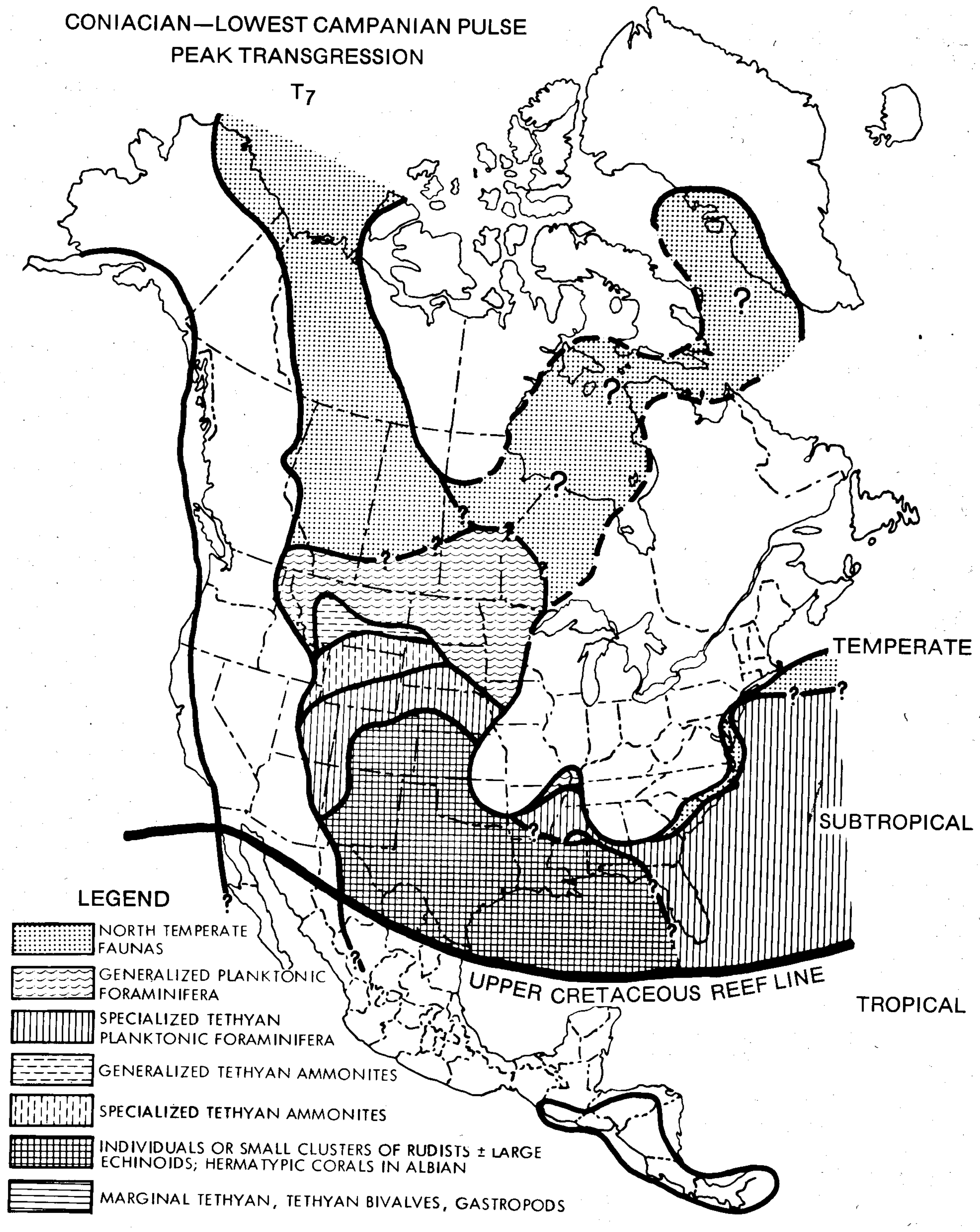

Figure 10. Generalized map of Western Interior Cretaceous Seaway of North America during peak Coniacian-Late Santonian fourth-order transgressions within third-order Niobrara Eustatic Cycle. Map shows distribution of various Subtropical organisms (patterns keyed to lower left of diagram), defining extensive, short-term northward migration of Warm Temperate and Subtropical paleobiogeographic units into the seaway during rapid incursion of warm, normal marine waters at eustatic highstand. Compare with more normal paleobiogeographic distributions in Figure 7.

boundary to at least the Early Coniacian (Fig. 10) is indicated by these distributions.

(g) A second small regressive pulse (R_{7b}) occurred during the latest Coniacian and Early Santonian (zones of *Scaphites depressus, Clioscaphites saxitonianus,* and *C. vermiformis*); numbers and diversity decreased among specialized calcareous microplankton while a few typical, Subtropical elements persisted up to southern Wyoming, including some specialized planktonic foraminifers, rare *Durania,* and ammonites of the Family Texanitidae (*Texanites, Protexanites*). A slight southward retreat of the Subtropical-Warm Temperate climatic/biogeographic boundary into south-central Colorado is indicated.

(h) The third major Tethyan biotic incursion (T_{7c}; Fig. 4), associated with one of the two most extensive fourth-order transgressions of the Niobrara cycle, is represented by late Middle Santonian chalks (*Clioscaphites choteauensis* Zone) in the central and southern Interior seaway. These contain diverse, warm water, calcareous microplankton up to south-central Wyoming (Kent, 1967; Frerichs *et al.*, 1975), large rudists (*Durania*) to Colorado and Kansas, and texanitid ammonites into Wyoming. Generalized calcareous microplankton reached central Canada (Fig. 10); the Subtropical-Warm Temperate biogeographic boundary again shifted 500 to 1000 miles (800 to 1600 km) northward in 0.5 Ma or less.

(i) A minor one-Ma regressive pulse (R_{7c}; Fig. 4) occurred during the Late Santonian (zones of *Desmoscaphites erdmanni* and *D. bassleri*) and is represented by widespread return to deposits of shaly chalk and calcareous shale. The calcareous microbiota, rudist bivalves, and Tethyan ammonites all declined in numbers as the Subtropical – Warm Temperate biogeographic boundary retreated into southern Wyoming, northern Colorado, South Dakota and Nebraska. However, generalized planktonic foraminifera remained as far north as southern Canada, indicating little expansion of the Cool Temperate biota during this regression.

(j) A final northward migration of Subtropical biotas during the Coniacian – Santonian transgressive event occurred during the latest Santonian and earliest Campanian (Zone of *Scaphites hippocrepis*). It is represented by northward spread of pelagic chalks and limestones, and by a small increase in planktonic foraminiferal numbers and diversity including an increase in diversity of keeled species. Gulf Coast ammonites (*Scaphites hippocrepis – S. leei* plexus; Cobban, 1969) reached northeastern Alberta and rudists (*Durania*) immigrated as far as southern Colorado. The Subtropical - Warm Temperate boundary reached southern Wyoming. This pulse was notably less extensive than previous T_7 incursions.

(k) An abrupt (0.5 Ma) decline in numbers and diversity of calcareous microbiotas, and rapid southward emigration of specialized, Subtropical macrofaunas and keeled planktonic foraminifera, occurred during the latest Santonian – Early Campanian regression (R_{7d}; *Haresiceras placentiforme* Zone). The Subtropical Gulf Coast-Warm Temperate Southern Interior Subprovince boundary shifted southward about 600 miles (1,000 km) into Texas in less than one million years. Cool Temperate biotas of the Northern Interior Subprovince expanded once again into the northern United States to a position similar to that in Figure 7 by middle Early Campanian.

Thus, the Coniacian – Santonian transgressive peak (T_7; Fig. 4) in the Western Interior seaway was characterized by fluctuating levels of Subtropical Tethyan biotic influence throughout its 5 Ma history; each fluctuation was linked to small fourth-order transgressive-regressive episodes. Alternating northward migrations of Subtropical elements to southern Wyoming, and their subsequent retreat to southern Colorado, mark these fluctuations of the Gulf and Atlantic Coast – Southern Interior Subprovince boundaries. Figure 4 suggests that each Subtropical incursion lasted 0.5 Ma or less; southward retreat of the Marginal Tethyan boundary was a slower process. Marginal-Tethyan influence was strongest between the Early Coniacian and the Middle Santonian, and gradually weakened during the Late Santonian and Early Campanian, with retreat of the Subtropical – Warm Temperate paleobiogeographic boundary into Texas associated with falling sealevel.

The Early Late Campanian Incursion. A moderately extensive and rapid (2.5 Ma) marine regression (R_{7d}; Fig. 4) followed the Coniacian – Santonian Subtropical incursion, causing emigration of Marginal Tethyan and Warm Temperate biotas to the Texas Coastal Plain. This regression terminated during the middle Early Campanian (Fig. 4). A number of smaller transgressions followed during Campanian – Maastrichtian time (T_8 – T_{10}; Fig. 4), reflecting additional eustatic fluctuations, but within the Western Interior Basin none were of the magnitude of the previous events. Nevertheless, each ensuing transgression (eustatic rise) in the Western Interior Basin was characterized by rapid northward immigration of Subtropical and Warm Temperate biotas and the paleobiogeographic units which they occupied.

A small incursion of Subtropical faunal elements occurred during the early part of the Late Campanian (Fig. 11), near the transgressive peak of the Claggett Cyclothem (T_8, Fig. 4). Transgression and the first Subtropical biotic incursions began in the late Early Campanian (*Baculites obtusus* Zone) and peaked in the early Late Campanian (*B. mclearni, B. asperiformis,* and *B.* sp. smooth zones). Subtropical immigrants at peak-transgression included the *Trachyscaphites spiniger* ammonite lineage in Wyoming, scattered rudistid bivalves ("*Icthyosarcolites*" *coralloidea* Hall and Meek) in central Montana, and generalized planktonic foraminifer, in central Wyoming (Mello, 1971). Stenothermal, keeled, planktonic foraminifer occurred in abundance only near the southern aperture of the seaway. At maximum incursion (early Late Campanian), the Subtropical-Warm Temperate boundary lay across northern Wyoming, southern Montana and central South Dakota (Fig. 11) – the average northern range of Subtropical ammonites, rudists, and planktonic foraminifera. Sohl (1967, 1971) noted that the Subtropical gastropod genera *Trachytriton* and *Desmieria* have a similar Campanian distribution. The approximate duration of this Tethyan pulse was 1.25 Ma (Fig. 4). A prominent regression followed (R_8; Fig. 4) causing southward retreat of many but not all Subtropical elements. Mello (1971) noted abundant planktonic foraminifer in central Wyoming during the Claggett regression (*B. gilberti – B. scotti* zones); rare Subtropical gastropods and rudists remained in the southern and central part of the seaway during this regression.

The Middle Late Campanian Tethyan Incursion. The last major transgression in the history of the Western Interior seaway began and peaked in the middle Late Campanian (*Didymoceras nebrascense* through *Baculites compressus* zones; Bear-

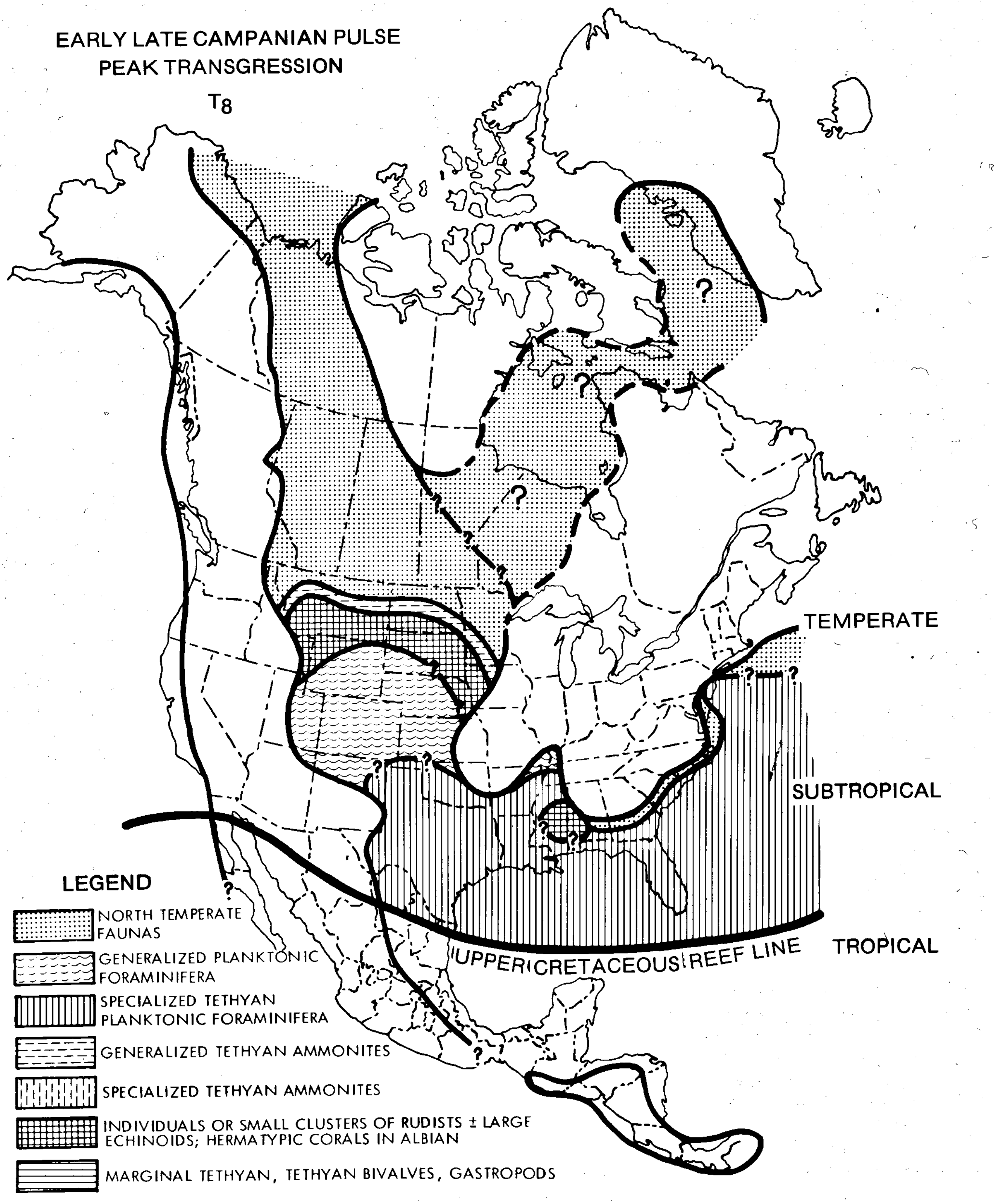

Figure 11. Generalized map of Western Interior Cretaceous Seaway of North America during peak early Late Campanian transgression associated with the Claggett Eustatic Cycle. Map shows distribution of various Subtropical organisms (patterns keyed to lower left of diagram), defining extensive, short-term northward migration of Warm Temperate and Subtropical paleobiogeographic units during rapid incursion of warm, normal marine waters into the seaway at eustatic highstand. Compare with more normal paleobiogeographic distributions in Figure 7.

paw Cyclothem; Kauffman, 1977a). A major incursion of subtropical biotas accompanied the transgression, reaching central Canada (Fig. 12), and included rudistid bivalves ("*Icthyosarcolites*"), Subtropical gastropods (*Trachytriton, Desmieria;* Sohl; 1967, 1971), and generalized planktonic foraminifer (Mello, 1971) during and just following peak-transgression (*B. compressus* Zone). The bulk of the faunal evidence suggests that the Subtropical (Gulf and Atlantic Coast) – Warm Temperate (Southern Interior) boundary extended across northern Wyoming. A major regression followed (R_9; Fig. 4), and all Subtropical biotas disappeared from the Western Interior during the latest Campanian to Early Maastrichtian with southward expansion of Cool to Mild Temperate biotas into the United States. The middle Late Campanian incursion lasted one Ma; the main pulse was less than 0.5 Ma long (Fig. 4).

The Maastrichtian Tethyan Incursion. The Early and Middle Maastrichtian marks the major M_9 regression (Fig. 4) of epicontinental seas from the Western Interior Cretaceous Basin. This regression was interrupted by a minor transgressive reversal and brief northward spread of warm-water biotas during the late Early to Middle Maastrichtian (*B. clinolobatus* Zone). Mello (1969) reported an assemblage of mostly generalized, planktonic foraminifera in South Dakota, coincident with the peak of this minor transgression. Speden (1970) reported sparse rudists ("*Icthyosarcolites*") in the Lower Fox Hills Formation along with the warm-water bivalve *Parapholas.* The northward extent of these more typical Subtropical elements is shown in Figure 13. The evidence does not suggest a major displacement of the Subtropical – Warm Temperate Boundary at this time; possibly it reached northern New Mexico and southern Colorado. The duration of this incursion was about 0.25 Ma.

Summary

Five major and five minor northward incursions of southern Warm Temperate and Subtropical organisms from the Gulf and Atlantic Coast Subprovince far into the Western Interior Seaway of North America were predominantly associated with short intervals around peak-transgressions, reflecting eustatic highstands. Isotopic, sedimentologic, and paleobiologic data suggest that relatively abrupt increases in temperature and salinity, and re-establishment of vertical circulation, immediately preceded and/or accompanied these incursions, but that somewhat more gradual declines in temperature and salinity terminated them. This in turn suggests that warm Subtropical surface-waters rapidly flooded northward into the epicontinental basin after a prolonged period of eustatic rise which finally reached some critical threshold of depth, overcoming circulational barriers formed in the constricted, partially silled, southern aperture of the Western Interior Seaway. Prior to and just after such incursions, geochemical and paleobiological data strongly suggest that the Western Interior Seaway was slightly brackish, broadly oxygen-restricted, and wholly within Temperate climatic belts.

Evidence for rapid northward incursions of Subtropical organisms is mainly found in: widespread pelagic carbonates, reflecting floods of calcareous microplankton (including stenothermal, keeled, planktonic foraminifera) and calcareous benthonic foraminifera; isolated specimens or small clusters of rudist bivalves; diverse Subtropical gastropods and bivalves; larger irregular echinoids; rare hermatypic colonial corals; and among Tethyan ammonites. These Subtropical elements, and numerous warm-water, cosmopolitan taxa appeared, immigrated northward for considerable distances, and then emigrated from the basin within short periods of time (0.25 to 2.5 Ma intervals). Regressions greatly restricted or eliminated Subtropical biotas from the Western Interior Seaway, although a few more adaptive taxa remained during lesser regressive pulses of the Coniacian and Santonian. The paleobiogeographic fluctuations of the Central Interior – Southern Interior Subprovince boundary, and the Southern Interior – Gulf and Atlantic Coast Subprovince boundary, correlate with migrations of the Subtropical and Warm Temperate climatic zones from the Gulf Coastal Plain into the Western Interior Basin and back over distances as great as 1,300 miles (2080 km).

In general, there seems to be a patterned biotic response to these incursions of subtropical Tethyan biotas, and similarity in the biotas of each incursion – i.e., one to two genera of rudists, one to five genera of Subtropical ammonites, a moderate number of other molluscan genera, one to two hermatypic coral and larger echinoid genera, floods of planktonic and benthonic, calcareous microbiotas, and only moderately complex community structure. Many communities were composed equally of Subtropical, cosmopolitan and eurytopic Temperate organisms during these incursions. The duration of each incursion was too short, and Tropical environmental influence too marginal to allow development of complex Tethyan ecosystems in the Western Interior. There also seems to have been a relatively consistent, north to south, geographic distribution pattern of warm-water faunal elements during these incursions. This probably reflects variations in thermal tolerance among Warm Temperate to Subtropical organisms versus the nature of the thermal gradient in the Western Interior Seaway. Thus, generalized (eurythermal) planktonic foraminifera and nannoplankton usually extended farthest to the north, miscellaneous Subtropical bivalves and gastropods next-farthest, ammonites of Tethyan affinities next, specialized (keeled) planktonic foraminifera next, and hermatypic corals, radiolitid rudists, and larger echinoids had the least northerly range during any incursion. Exceptions exist as apparent ecological tolerances shifted in groups through time (e.g., rudists) or due to gaps in biogeographic documentation.

In many cases these rapid paleobiogeographic incursions were associated with other major changes in the biota, such as major extinctions, breakdown of ecological structure, increases in evolutionary rates, and high levels of endemism.

EVOLUTIONARY RESPONSE TO PATTERNS OF PALEOBIOGEOGRAPHIC CHANGE

Kauffman, in his analyses of evolutionary rates for Western Interior Cretaceous Mollusca (1972, 1977b, 1978), noted that in virtually all lineages studied, rates of evolution were primarily controlled by the ecological features of each group, such as: trophic strategy; habitat needs; adaptive breadth (degree of

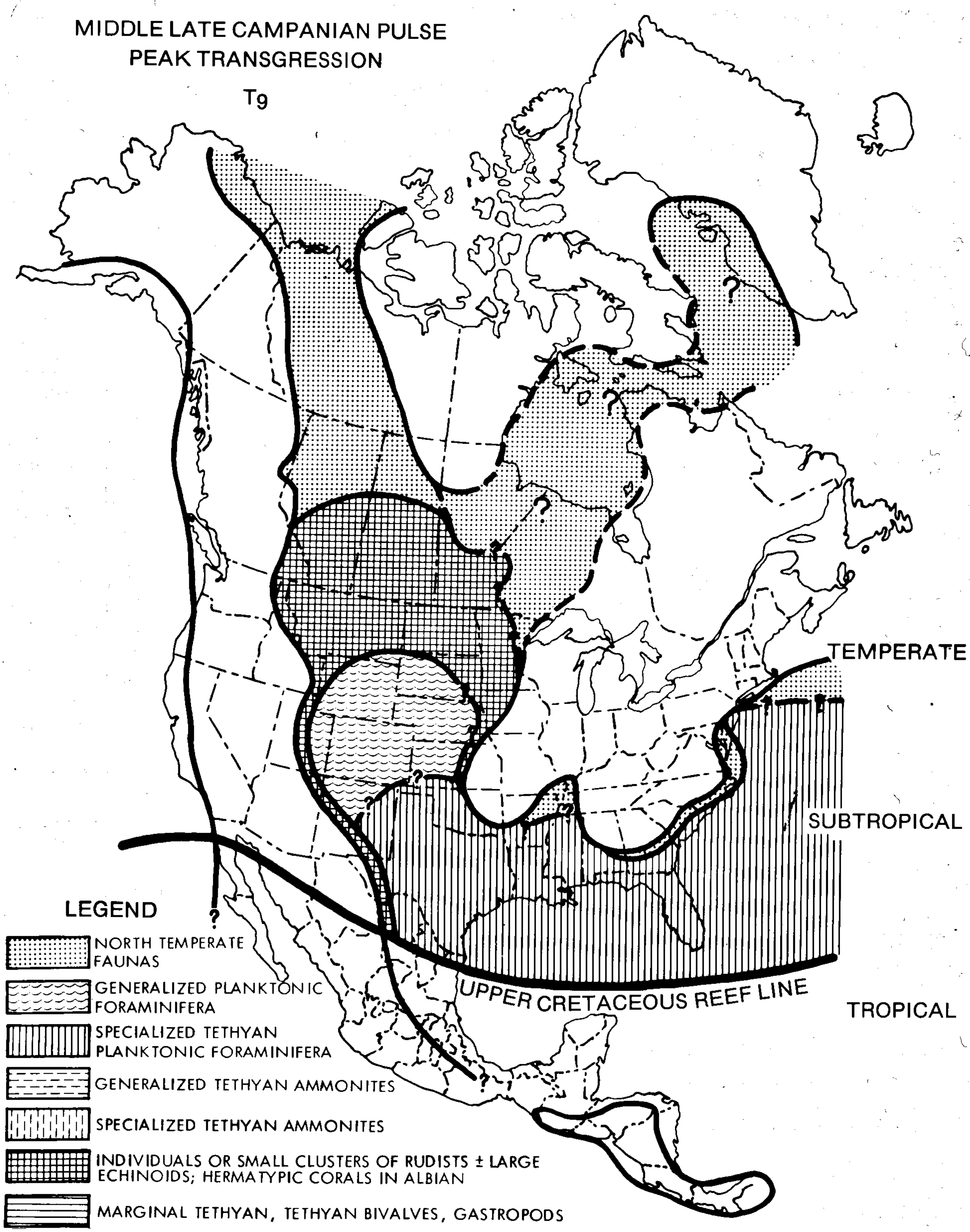

Figure 12. Generalized map of Western Interior Cretaceous Seaway of North America during peak middle Late Campanian transgression associated with the Bearpaw Eustatic cycle. Map shows distribution of various Subtropical organisms (patterns keyed to lower left of diagram), defining extensive, short-term migration of Warm Temperate and Subtropical paleobiogeographic units during rapid incursion of warm, normal marine waters into the seaway at eustatic highstand. Compare with more normal paleobiogeographic distributions in Figure 7.

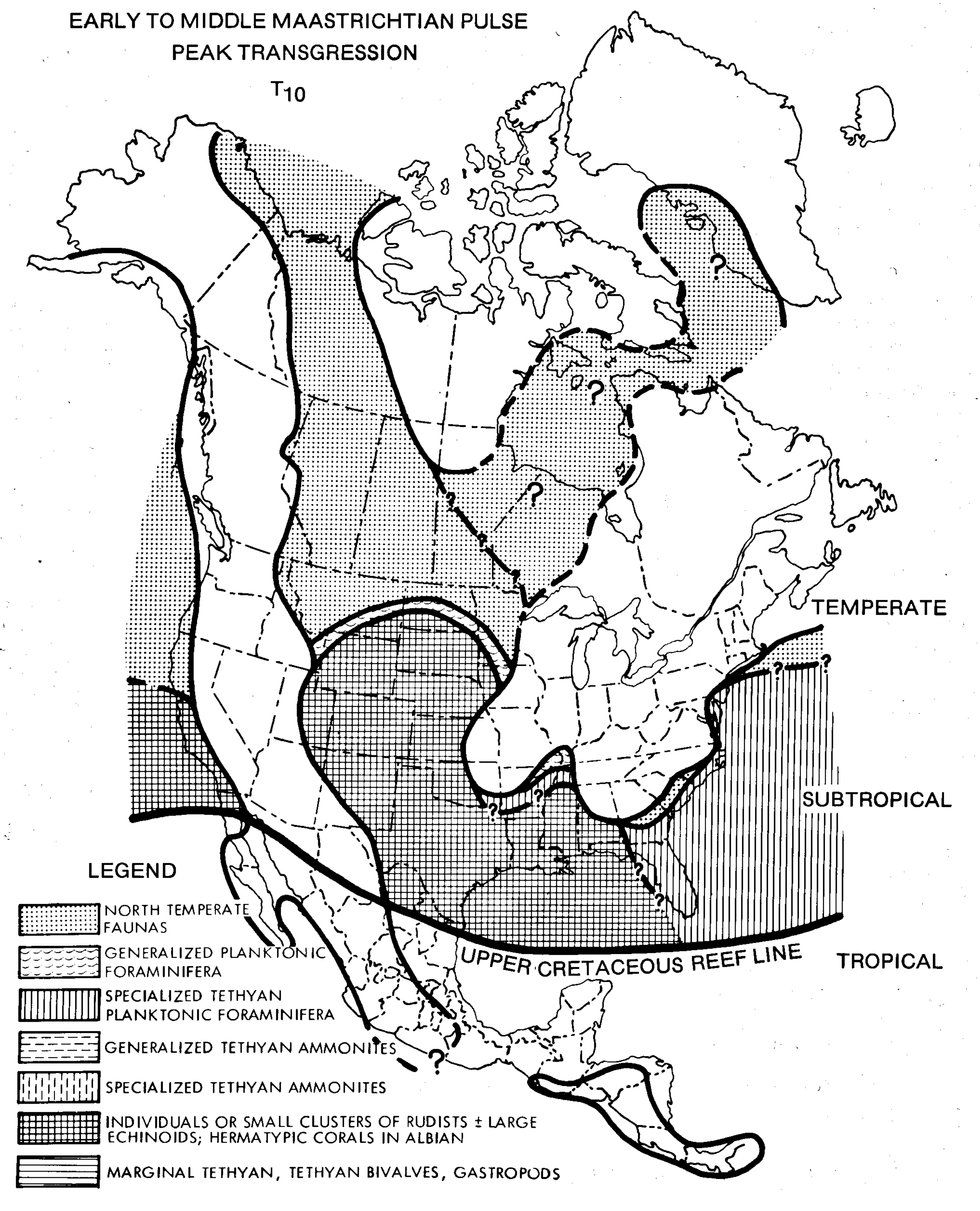

Figure 13. Generalized map of Western Interior Cretaceous Seaway of North America during a small Middle Maastrichtian eustatically-generated transgression associated with deposition of the Fox Hills Sandstone. Map shows distribution of various Subtropical organisms (patterns keyed to lower left of diagram), defining extensive, short-term migration of Warm Temperate and Subtropical paleobiogeographic units during rapid incursion of warm, normal marine waters into the seaway at small eustatic highstand. Compare with more normal paleobiogeographic distributions in Figure 7.

eurytopy *vs.* stenotopy); degree of habitat protection from unpredictable perturbations; and by the rate and magnitude of biological stress placed on these lineages through time by shifting physical, chemical, and biological factors of the environment. These initial analyses showed that virtually all episodes of rapid evolution recorded for different Cretaceous lineages were associated with peak eustatic rise in sealevel (peak-transgression) and throughout regression. These were times of rapid environmental changes followed by longer deterioration of marine habitats through loss or great restriction of prime niches; diminished ecospace; declining salinity, temperature and, sporadically, oxygen in the seaway; and by onset of highly turbid shallow-water conditions with increasing competition among surviving taxa for resources and habitats. Thus, in general, stenotopic, shallow-marine organisms, especially epibenthic and neritic taxa, were most affected by major fluctuations in sealevel, temperature, salinity, oxygen, turbidity, trophic resources, habitat size, and niche diversity. They were first to respond to eustatically related changes during peak-transgression and early regression. More eurytopic taxa did not undergo rapid evolution and extinction until high stress levels had been reached, as during the most rapid oceanographic changes associated with peak-transgression, or during the last phases of a major eustatic fall and widespread epicontinental regression. Some highly adapted taxa (e.g., intertidal and brackish water forms), and others with highly protected niches (deep burrowing or deep water taxa), showed little change in association with sealevel fluctuations.

Equally important was the documentation of major changes in evolutionary rates *within* lineages (Kauffman, 1977d, 1978) in direct relation to the rate and intensity of environmental change causing biological stress. With these relationships broadly documented, we can now turn our attention to paleobiogeographic impact on rates and patterns of evolution within the Western Interior Seaway.

Two major kinds of paleobiogeographic controls on Cretaceous evolutionary history can be envisioned in the seaway, one short-term and one longer-term. (1) The effect, during peak eustatic rise of sealevel, of major stress placed on Western Interior biotas due to rapid changes in oceanographic factors (e.g., temperature, salinity and oxygen). This was amplified by ecological disruption of the normal Western Interior biota through abrupt northward displacement of Temperate climatic belts and by the broad competitive boundaries established between Mild to Cool Temperate resident biotas and rapidly immigrating Warm Temperate to Subtropical biotas of the Gulf and Atlantic Coast Subprovince and the Caribbean Province. (2) Longer-term disruption of Western Interior ecosystems at major boundaries of paleobiogeographic units, such as the broad ecotonal zones of intermixing between discrete biotas of the Northern, Central, and Southern Interior Subprovinces, and between these Temperate Zone biotas and the Subtropical biota of the Gulf and Atlantic Coast Subprovince of the North American Province (Fig. 7; Kauffman, 1973). These two effects are difficult to separate in some cases.

Several tests have been made (Kauffman, 1972, 1977d, 1978) in an attempt to relate evolutionary rates to sealevel changes among Cretaceous molluscs of the Western Interior and Gulf Coast (Fig. 14 summarizes data); these analyses utilize number of species arising within lineages per million years as a measure of evolutionary rates (Kauffman, 1978, Fig. 1). Whereas these data clearly show that the highest evolutionary rates for many groups occurred during middle to late regressive stages of eustatic fall (e.g., Kauffman, 1972, Figs. 1-5; 1977d, Figs. 5-7; Figs. 3-5) associated with rapidly deteriorating epicontinental marine environments and loss or restriction of many prime habitats (i.e., high stress conditions), the second highest peaks of evolution in these data occur just before or during peak transgression, associated with rapid environmental and paleobiogeographic fluctuations. For example (Fig. 14), Kauffman has shown (1972, 1977d, 1978) that the middle to peak-transgressive phases of the Cenomanian eustatic rise (T_6; Fig. 4) are times of especially rapid speciation among many lineages of Bivalvia (*Nucula*, Tellinidae, *Yoldia, Cymbophora, Callistina, Inoceramus, Mytiloides, Camptonectes* and *Pycnodonte*), as well as among certain lineages of scaphitid ammonites. Kauffman has further shown unusually rapid to punctuated evolution in morphologic features of the *Inoceramus pictus* lineage during the latest Cenomanian (1977d, Fig. 4). These bursts of evolution coincide with the interval of greatest oceanographic and paleobiogeographic change during eustatic rise, as determined from geochemical, sedimentologic and biologic data. Important but less spectacular evolutionary peaks were also documented near the peak Coniacian-Santonian rise of sealevel (T_7; Fig. 4) for the bivalve lineages of *Protodonax* (intertidal), *Cremnoceramus,* and the ammonite genera *Baculites, Scaphites, Pteroscaphites,* and *Clioscaphites.* Peak Campanian transgressions show increasing evolutionary rates among the bivalves lineages of *Thyasira, Protodonax, Endocostea, Platyceramus* and *Pycnodonte* (Kauffman, 1978, Figs. 3-5) and the ammonites of the *Trachyscaphites* and *Hoploscaphites* lineages (Kauffman, 1977d, Fig. 6 modified to show sealevel highstand in Santonian and late Early Campanian).

Similar analyses of evolutionary rates among Cretaceous Mollusca of the Texas Gulf Coast (Kauffman, 1972, Figs. 1-4) strongly support observations from the Western Interior that abrupt paleobiogeographic and environmental changes around eustatic highstand and peak-transgression result in accelerated speciation rates. Analyses of 18 lineages of marine gastropods and 11 lineages of bivalves from the Gulf Coast show that the highest evolutionary rates for both classes and virtually all tested lineages occur at and just after peak-transgression of the late Early Campanian eustatic rise (T_8; Fig. 4); a strong secondary peak in bivalve evolution occurs early in the Late Campanian to lower Maastrichtian regression (R_9; Fig. 4), in association with a small fourth-order Early Maastrichtian transgressive peak. The stronger evolutionary effect of these maximum transgressions in the Gulf Coast may represent larger-scale thermal changes at the transgressive peak because of closer proximity to the migrating Subtropical-Warm Temperate climatic boundary. All new data that have been generated on lineage evolution in the Gulf and Western Interior biotas support these early observations.

I conclude from these extensive data that abrupt changes in marine environments (rapid fluctuations in temperature, oxygen, and salinity), and in the position of paleobiogeographic boundaries as they rapidly migrated northward across the Western Interior Seaway at peak eustatic rise, have severely stressed marine biotas of these areas, driving evolutionary rates upward within many lineages. It is difficult to sort out the physico-chemical stresses from those inherent in biological competition set up by immigration and establishment of ecologically disrupted ecotones, or from migrations of paleobiogeographic units over hundreds to more than 1000 miles (1600 km) during one to three million-year intervals. Nevertheless, the distribution of the data showing rapid evolution clustered tightly around transgressive peaks and limited to the known range of paleobiogeographic mixing (Sohl, 1967, 1971), or ecotone, strongly suggest at least a partial control on evolutionary rates due to biological stress related to rapid shifts in paleobiogeographic units.

A second biogeographic control on evolutionary rates and patterns among Cretaceous biotas is related to the establishment of broad paleobiogeographic ecotones at the junctions of Western Interior and Coastal Plain subprovinces. Though dynamic in the sense of broad and frequent north-south migrations, these mixing zones of Temperate and Subtropical biotas persisted for the 35 Ma history of the connection between northern and southern arms of the seaway. Unlike modern biogeographic ecotones, which extend for only tens of miles on either side of provincial boundaries, Cretaceous ecotones of the Western Interior were broad and graded over 500 to 1000 miles (800 to 1600 km, e.g., Colorado to Montana in the Campanian; Sohl, 1967, 1971) during much of their history, completely encompassing the Central Interior Subprovince. During major paleobiogeographic shifts, as near peak eustatic rise and transgression, the entire ecotone moved hundreds of miles north or south, and expanded or contracted in size. These perturbations should have had a profound effect on evolutionary history of Cretaceous marine biotas, as should the very existence of large biogeographic ecotones in the seaway.

Biogeographic units are expanded ecological units composed

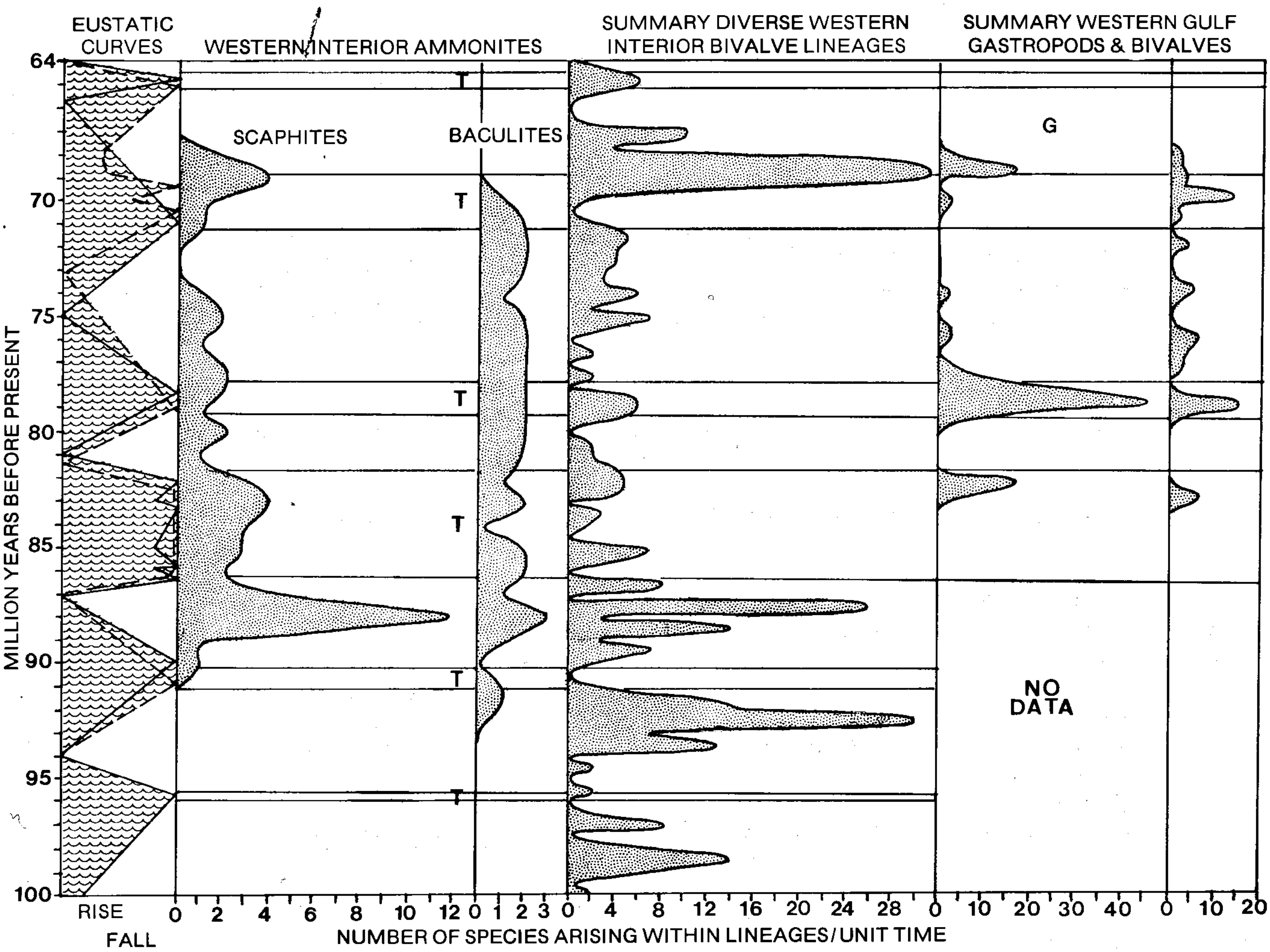

Figure 14. Summary diagram of molluscan evolutionary rates, as defined by number of species arising within single lineages per million-year interval, plotted against third-order Cretaceous tectonoeustatic cycles of the Western Interior Seaway (solid line) and western Gulf Coastal Plain (dashed line) (data from Kauffman, 1972, 1978, 1979). Note high correlation of episodes of rapid evolution with: (a) high-stress conditions during middle and late phases of eustatic fall and epicontinental regression, and (b) with rapid thermal, salinity, and dissolved oxygen fluctuations associated with warm water incursions during late transgressions and near eustatic highstands.

of numerous, at least broadly structured communities. For this reason one could predict that both community and biogeographic ecotones are zones of biological competition between similarly adapted taxa from discrete bounding communities and are thus biologically stressed and ecologically disrupted; these conditions favor increased endemism and more rapid evolution. Data exist from modern marine ecotones to support this contention. Newman (1979) and Spivey (1981) have demonstrated among living barnacles of the Pacific Coast and Gulf of Mexico that biogeographic ecotones with strong environmental gradients are characterized by extensive faunal mixing, lower than normal population size for many taxa (reflecting competition for the same space and resources), the highest levels of endemism for the group, and the presence of refugia species in open competition with species that had previously displaced them in well-structured ecosystems. Consequently, diveristy is higher than normal for barnacles in biogeographic ecotones.

These limited observations suggst a hypothesis which might be applied to understanding the evolutionary history of Cretaceous biotas in the Western Interior of North America, i.e.: Ecotones are zones of disruption of ecosystems because of the broad competition between similarly adapted taxa from different communities or biogeographic units in the same space – the zone of biogeographic overlap. They comprise a stressful environment, yet offer opportunities for new and unique adaptations because of the incomplete and inefficient use of ecospace made possible by establishment of a broad competitive boundary. This situation fosters the origination and rapid evolution of endemic taxa specifically adapted to ecotone niches. On the limited scale of modern ecotonal boundary zones this may result in a small number of endemics (ecotonal species) with restricted population size and geographic range; but during the Phanerozoic when climatic gradients, biogeographic boundary-zones, and thus ecotones were much broader and stabilized over longer periods, these ecotones may have acted as major centers of evolution among more widely spread endemic stocks. If so, they are extremely important to evolutionary theory, and may partially explain the broad variations in evolutionary rates and patterns observed for the biotas of the Western Interior Cretaceous Seaway (Kauffman, 1962, 1977d, 1978) and elsewhere. This hypothesis is testable with the extensive evolutionary data and high-resolution stratigraphy available for the Western Interior Cretaceous Seaway.

As a basic test of this hypothesis the principal biogeographic ranges of most Western Interior endemic molluscs (data from numerous sources) have been plotted against the average distribution of Temperate biogeographic subprovinces in the Western Interior (Fig. 7); the areal extent of this center of Western Interior endemism overlaps both major paleobiogeographic boundary zones in the center of the basin and extends north well into Canada, generally supporting the hypothesis that the boundary zones are a major center of endemic evolution.

The northern extension of this endemic center beyond the Mild Temperate-Cool Temperate biogeographic boundary seems puzzling at first, but the Campanian data of Sohl (1967; Fig. 7) clarify this in showing that the main zone of biogeographic overlap of gastropod taxà partially defining the broad

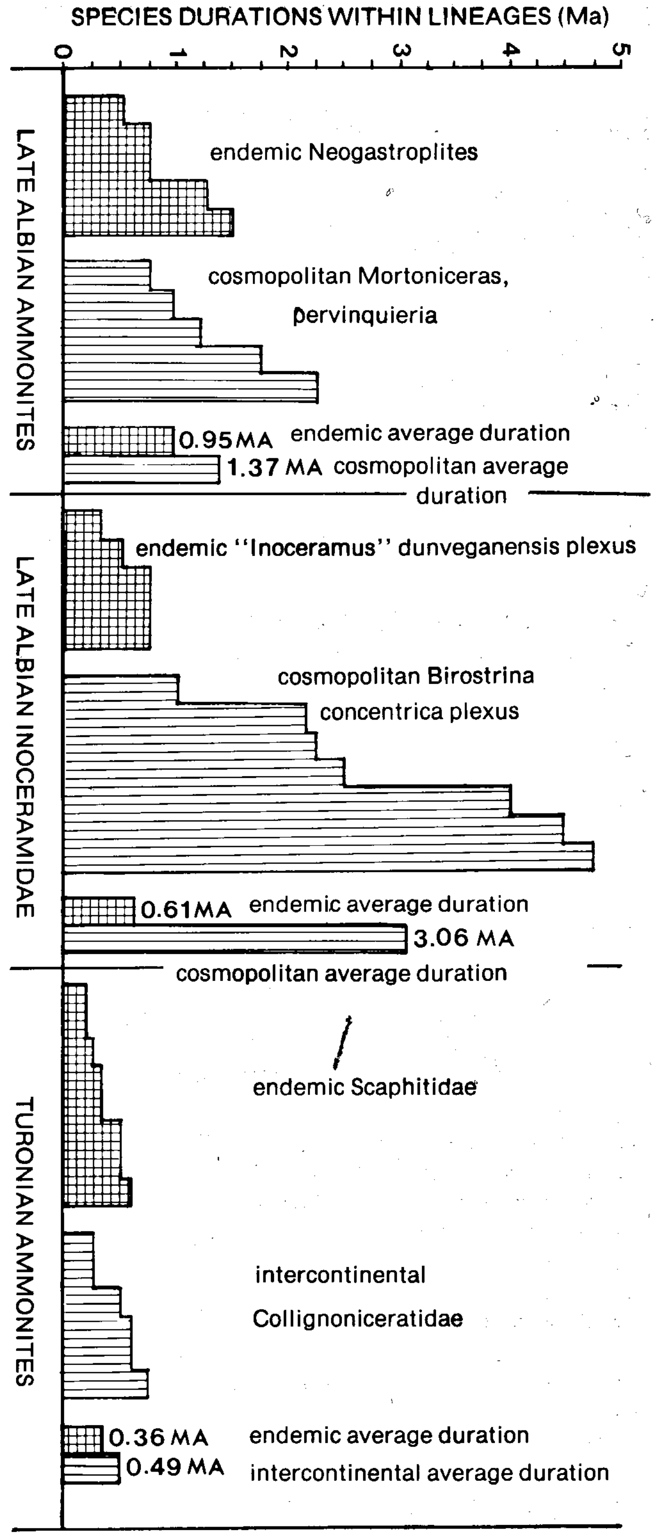

Figure 15. Comparative evolutionary rates between intercontinental or cosmopolitan molluscs and those of the Western Interior paleobiogeographic ecotones, as measured by average species durations within lineages of ammonites and inoceramid bivalves. Note higher rates of evolution for endemic ecotonal lineages arising at the competitive, biologically stressed boundaries between paleobiogeographic subprovinces.

ecotone between the Northern Interior (Cool Temperate) Subprovince and the Southern Interior (Warm Temperate) Subprovince, actually extends from central Colorado well into Montana and, probably, southern Alberta. My own unpublished data from Cretaceous Bivalvia supports Sohl's observations completely. This northern offset of the ecotone from the Central Interior-Northern Interior Subprovince boundary probably reflects the dominance of southern warm-water surface currents over deeper, northern cool-water counter-currents in the seaway. This hypothesis is further supported by the relatively greater magnitude of northward Subtropical Tethyan biotic incursions during peak-transgression, as opposed to the more limited southward migration of Cool Temperate organisms between transgressive peaks. Thus, the general biogeographic distributional patterns and close spatial correlation through time of both endemic lineages and the Western Interior ecotones support the hypothesis that these zones of biogeographic overlap and ecosystem disruption fostered evolution of unique endemic taxa over a broad area in the Cretaceous, and possibly at other times during the Phanerozoic.

A second test of the hypothesis can be made by plotting the evolutionary rates of endemic taxa within these ecotones against those of contemporaneous taxa with broader Temperate Zone to cosmopolitan biogeographic distribution. Lineages of ammonites and inoceramid bivalves, representing the best studied molluscs for the Western Interior Seaway with a broad range of biogeographic distributional patterns, were selected for testing. Figure 15 shows the results of this analysis; in every case, evolutionary rates of endemic lineages arising within the biogeographic ecotone were more rapid than those of contemporaneous and ecologically similar lineages with broader paleobiogeographic ranges. Future analyses will focus on the timing and biogeographic migration patterns of evolution in these endemic centers.

CONCLUSIONS

Analyses of Cretaceous paleobiogeographic distribution patterns in the Western Interior Seaway of North America, utilizing modern concepts of biogeography and similar analytical levels of endemism to define biogeographic units, reveals the presence of three subprovinces, representing (north to south) Cool Temperate, Mild Temperate and Warm Temperate climatic zones. These subprovinces were definable during most of the history of the seaway. These subprovinces equate in general biotic character to modern Atlantic Coastal provinces between Nova Scotia and the Carolinas plus the northern Gulf of Mexico. Their greater biogeographic spread, compared to modern analogs, reflects a broader and warmer climatic gradient during the Cretaceous, lacking cold polar zones. Whereas an average distributional pattern for these subprovinces can be plotted (Fig. 7), reflecting conditions during most early to mid-transgressive and mid- to late-regressive eustatic episodes, these subprovinces were highly dynamic in space and time, especially during peak-transgression (eustatic highstand).

Each transgressive peak for third-order tectonoeustatic cycles in the Western Interior is characterized by a short (0.5-2.5 Ma) interval during which southern Warm Temperate and Subtropical taxa, biogeographic units, and ecotonal boundary zones migrated rapidly far to the north in the seaway, normally reaching the Canadian border or southern Alberta and Saskatchewan. Similar but lesser incursions of warm-water taxa are associated with some fourth-order transgressive peaks as well, suggesting possible eustatic control on these 1.5 Ma long events. The rapidity with which these migrations took place, displacing Temperate Zone subprovinces and their ecotonal boundaries northward, suggests some threshold effect at the southern end of the Western Interior Basin. Possibly, a structural and sedimentologic barrier or sill existed at the southern end of the seaway and was rapidly overstepped at some critical point in sealevel rise, allowing warm-water masses to flood quickly into the Interior. During these peak-transgressive intervals, a four-fold biogeographic division of the Interior seaway was possible, therefore, with the Gulf and Atlantic Coast Subprovince (Subtropical to very Warm temperate) migrating across the central and northern part of the United States interior, and Temperate subprovinces being displaced northward. Retreat of these warm-water biotas during sealevel fall was somewhat slower, but still took less than 1.5 Ma in most cases.

These migrations had a profound effect on the evolution of lineages and ecosystems in the Western Interior Cretaceous. In particular, the development and rapid migration of broad paleobiogeographic ecotones at subprovince boundaries, characterized by extensive overlap of southern warm-water and northern cool-water taxa and disruption of ecological structure, provided a biologically and physico-chemically stressed environment in which the origin and rapid evolution of endemic molluscan taxa were favored. Tests of this hypothesis are wholly positive. Plots of the biogeographic range of the ecotones *vs.* the principal regions where endemic taxa have arisen in the Western Interior Seaway show almost complete overlap (Fig. 7). Evolutionary rates of endemic taxa arising in these ecotonal zones are slightly to significantly greater than those of contemporaneous, co-occurring taxa with similar ecological requirements but broader biogeographic distribution. From these analyses, I conclude that paleobiogeographic ecotones were dynamic, in space and time; they migrated broadly and rapidly, were ecologically disrupted for long intervals, and thus presented unique opportunities for the origination and rapid evolution of initially endemic taxa. Biogeographic ecotones probably have been important centers for evolution throughout the Phanerozoic and are deserving of careful study in consideration of evolutionary theory.

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