Late Jurassic Paleoclimate Simulation—Paleoecological Implications for Ammonoid Provinciality

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During the Kimmeridgian and Tithonian stages (154.7–145.6 Ma) of the Late Jurassic, the Late Permian-early Mesozoic megacontinent Pangea was progressively fragmented by two rift systems that propagated westward out of the Tethys Sea and a third more persistent rift system that connected the Boreal and Tethys seas. By the late Tithonian, these major rift systems produced interconnected oceanic seaways that divided Pangea into four continental segments: North America, Eur-Asia, and northern and southern Gondwana. Increased rates of sea-floor spreading during the Jurassic reduced the volumetric capacity of ocean basins and produced a sea level rise through the period that culminated in the Late Jurassic.

The extensive marine shelf margins and epeiric seas hosted a widely distributed and diverse ammonoid fauna. Late Kimmeridgian and Tithonian ammonoids are reported from 47 localities worldwide. Ammonoids changed from cosmopolitan in the Kimmeridgian to strongly provincial by the late Tithonian. Warm to tropical water Tethys-Panthalassa Realm, comprised of several faunal provinces, occupied the eastern, central, northwestern, and southwestern portions of the Tethys Sea and both sides of the Panthalassa Ocean. By the early Tithonian, faunal communication existed between the northwestern Tethys Sea and the eastern Panthalassa Ocean through the proto-Gulf of Mexico. By the late Tithonian, faunal similarities between the southwestern and central Tethyan provinces and southeastern Panthalassa indicate the opening of the proto-Indian Ocean so that northern and southern Gondwana had become separate continents. A region of the equatorial Tethys that includes most of the present Arabian Peninsula contains neritic platform facies but lacks ammonoids. In high northern latitudes, cool to cold water faunas formed a Boreal Realm which extended westward across northern North America, Europe, and Siberia during middle and late Tithonian.

Late Kimmeridgian and Tithonian ammonoid distributions when compared with Late Jurassic paleoclimate simulations show likely causal relationships with sea surface water temperature and upwelling, and possibly shed light on the temperature limitations of ammonoids. Results from modeled seasonal sea surface temperature, sea ice distribution, precipitation-evaporation, and wind-driven upwelling permit the evaluation and quantification of paleoenvironmental factors favorable as well as pernicious for ammonoid distribution.

INTRODUCTION

Early in their studies of Late Jurassic ammonoids Neumayr (1871), Suess (1885–1909) and Zittel (1870) recognized the strong provincial distribution of many taxa. Suess, in fact, introduced the terms Tethys, Panthalassa, and Gondwana to help discuss these provincial distributions. Much of the data in these studies was used by Arldt (1919–1922) in his summary in "Handbuch der Palaeogeographie." Arkell (1956) and Arkell et al. (1957) in summaries of ammonoid taxonomy and stratigraphic distributions also included a discussion of the geographic distributions of ammonoid genera. With the general acceptance of paleogeographic reconstructions based on plate tectonics and sea-floor spreading, new perspectives were added to those earlier paleobiogeographic analyses of ammonoid distributions (Enay, 1973). The addition of a paleoclimate model for the Late Jurassic, which we attempt here, helps to explain additional aspects of the complex history of ammonoid distributions and the development of their provinciality.

In this study we used a general circulation model (GCM) called the Community Climate Model (CCM) version 0 developed at the National Center for Atmospheric Research, Boulder, Colorado. Our version of the CCM runs

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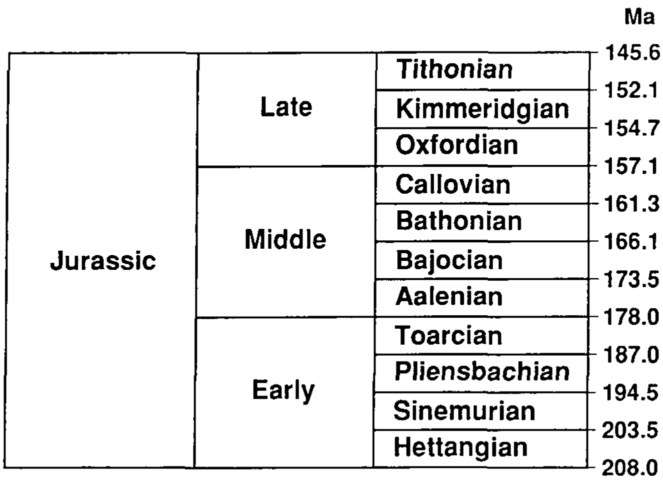

From Harland *et al.*, 1990

FIGURE 1—Subdivision of the Jurassic Period showing the time interval (Kimmeridgian and Tithonian) used in this study.

on a Cray supercomputer at Chevron Oil Field Research Company in La Habra, California. In this paper, we attempt to integrate the well-documented Late Jurassic ammonoid taxonomy and distribution with a paleoclimate simulation for the Kimmeridgian and Tithonian stages (154.7–145.6 Ma) with boundary conditions set for the beginning of this interval (Figs. 1, 2).

KIMMERIDGIAN AND TITHONIAN PHYSICAL WORLD AND CCM BOUNDARY CONDITIONS

Paleogeography

A progressively rising sea level throughout the Jurassic culminated in the Late Jurassic (Haq et al., 1988). The rise reflected an increased rate of sea-floor spreading as well as the flooding and disintegration of Pangea (Hallam, 1988). The paleoceanic setting for the Kimmeridgian and Tithonian world included: a Boreal and Austral sea in the respective high latitude hemispheres; a vast ocean called Panthalassa that covered approximately 165° of longitude; and the zonally-oriented tropical sea called Tethys from which emanated two narrow rift systems, one westward-trending and the other southwestward-trending (Fig. 2).

The two rift systems propagated westward out of the Tethys Sea as shown by paleogeographic reconstructions (Rowley, 1992; Scotese, 1991). A third persistent north-trending rift system connected the Boreal Sea with the Tethys (Ziegler, 1988). These started to fragment the Late Permian to early Mesozoic megacontinent Pangea by Late Jurassic time and became the sites of the major rifting events that produced oceanic seaways. These seaways separated Pangea into three major continental segments: North America, Eur-Asia, and Gondwana (Fig. 2). The paleogeography used for these simulations shows the relationships at the beginning of the Kimmeridgian (154.7 Ma) and was used as the land–ocean boundary conditions for the paleoclimate simulation. By late Tithonian time, Gondwana was separated by the southwestern rift system into two members, north and south.

Much of the Eur-Asian continent was flooded (Ziegler et al., 1983). The north-trending rift system (which included the North Sea) had existed in one form or another throughout Pangea's history (Ziegler, 1988), connected the Tethys to the Boreal Sea, and separated North America from Eur-Asia essentially along the mid-Paleozoic Taconic-Caledonide geosuture. In the Late Jurassic, this seaway was relatively deep, complex in detail, and narrow (Ziegler, 1988).

The rift migrating westwardly from the Tethys separated North America from Africa and South America, forming the embryonic central Atlantic and proto-Gulf of Mexico. The southwest rift system, followed by sea-floor spreading, separated Gondwana into a northern (Africa and South America) and a southern (India, Antarctica, and Australia) segment forming the proto-Indian Ocean.

Paleotopography

Because the CCM also requires a topographic component as another boundary condition, we have estimated paleotopography as land elevation in kilometers in 1 km intervals, up to 3 km (Fig. 3). Because orogeny and erosion change topography, qualitative and quantitative information for global Late Jurassic paleotopography is difficult to assemble. In this study, we estimated mountain range height in the latest Jurassic based on interpretations of Ziegler et al. (1983) and Scotese (1991) (Fig. 3).

MODEL DESCRIPTION

The evolution and specifics of this CCM were discussed in detail by Washington and Williamson (1977), Barron (1985), Barron and Washington (1984, 1985), Sloan and Barron (1989), Moore et al. (1992a), and references cited therein. The CCM uses thermodynamic and hydrodynamic laws applied to the atmosphere and has been shown to model present-day climate reasonably well (Bourke et al., 1977; McAvaney et al., 1978; Pitcher et al., 1983). The vertical dimension consists of nine atmospheric levels extending to 33 km in seasonal simulations. The modeled atmosphere extends through the troposphere and into the middle stratosphere. The horizontal dimension consists of 40 latitude by 48 longitude grid points with each grid cell having a resolution of 4.5° latitude by 7.5° longitude for a total of 1920 grid cells. The paleogeographic map (Fig. 3) is shown in model resolution format. This accounts for the blocky nature of the continental outlines. The paleotopography is likewise in this format and is illustrated and evaluated in Moore et al. (1992a, b).

We recognize that the Earth's orbital eccentricity, axial obliquity, and precession as well as its length of day and year have changed throughout geologic time. Further, the Sun's irradiation changes on a long-term, geological trend (White, 1977; Gilliland, 1989; Gérard, 1990), as well as periodic short-term cycles of 11 and 22 years and possibly

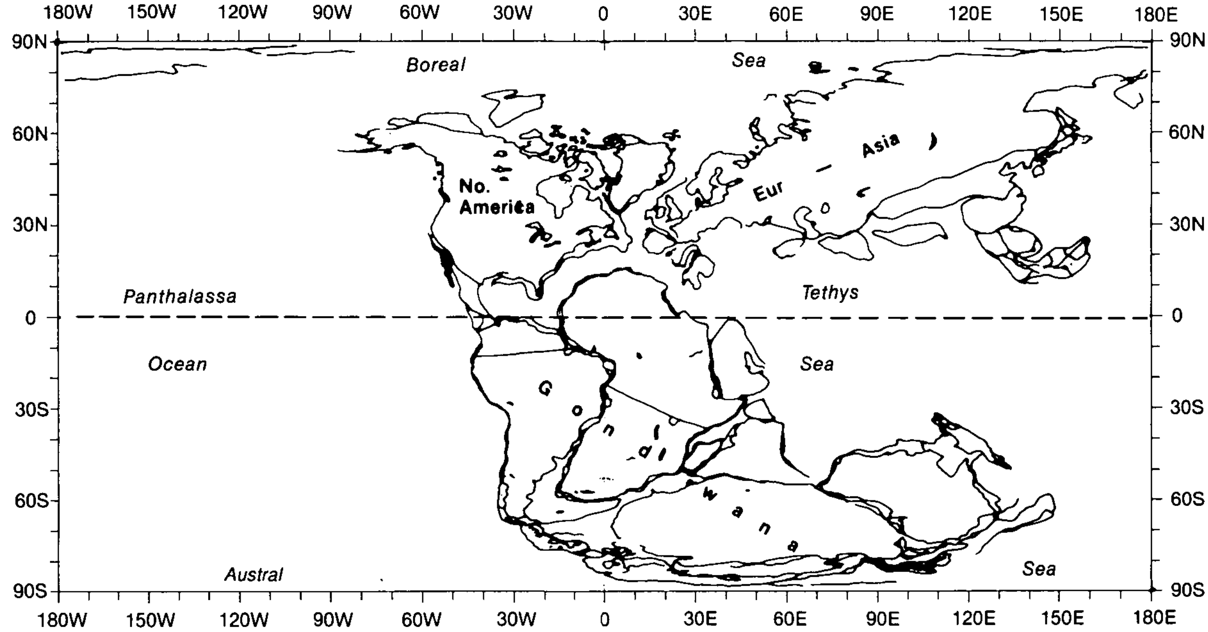

FIGURE 2—Kimmeridgian reconstruction using present-day continental outlines and identifying landmasses and water bodies referred to in text. Reconstruction based on Rowley (1991) and Ross and Ross (1983).

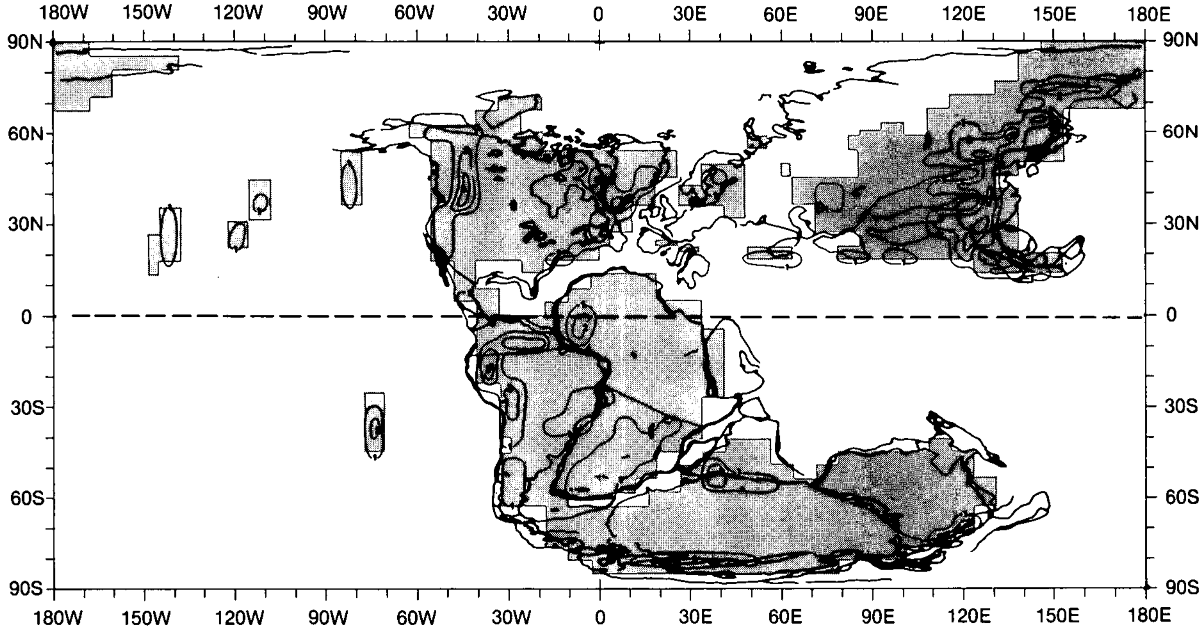

FIGURE 3—Kimmeridgian reconstruction and paleogeography in CCM model resolution format (4.5° lat. × 7.5° long.); land grid cells shaded. Present continental outlines shown for reference. Paleotopographic contours in km.

longer periods (Gérard, 1990; Baliunas and Jastrow, 1990; Reid, 1991). Stellar evolutionary theory predicts that solar luminosity has increased from about 70–75% of the current value over geologic time (4.5 Ga) (Gérard, 1990; Gilliland, 1989). However, questions about values, rates of change, and even the theory remain. Using the standard or linear model of increasing irradiance, the Sun in the Late Jurassic should have had 97.7% of the present Sun's luminosity. Reid (1991) showed variations in solar irradiance may have varied between 0.1% and 1% over the last few centuries, and possibly 0.6–0.8% between recent sun spot cycles. As all these variables are poorly constrained beyond the Pleistocene and, as the short-term variation of up to 1% in solar irradiation is in the same general range and magnitude as that calculated for the Late Jurassic using the linear model (2.3%) in this study,

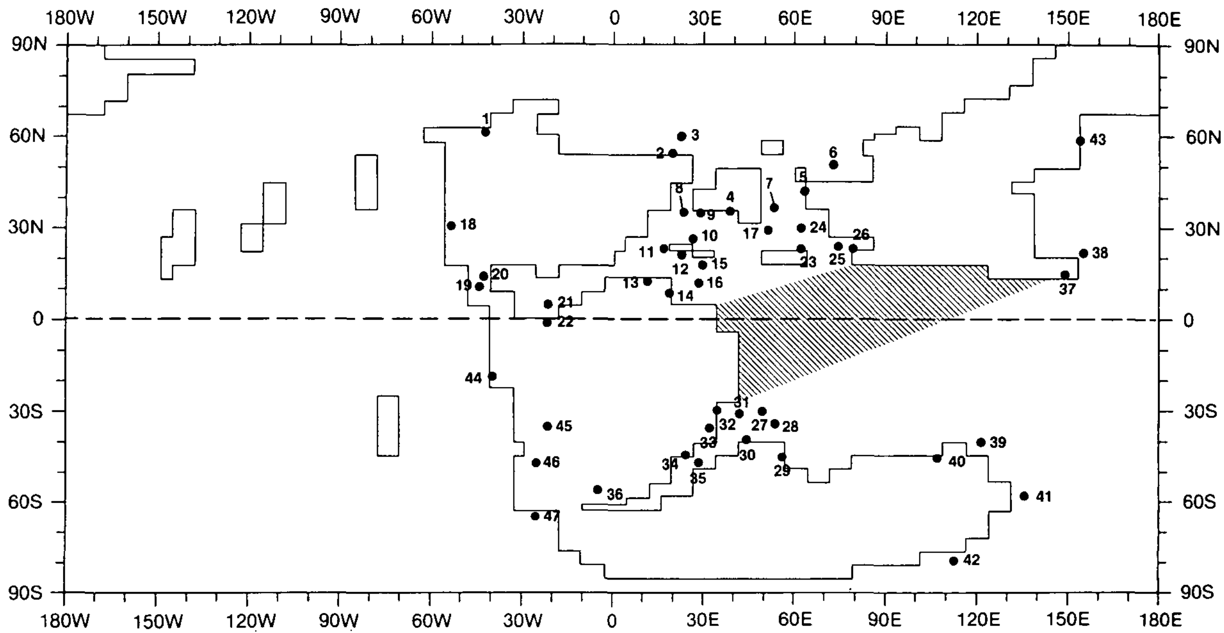

FIGURE 4—Kimmeridgian reconstruction with paleogeography in CCM model resolution (4.5° lat. × 7.5° long.) format. Distribution of Kimmeridgian and Tithonian ammonoid fossil localities are indicated. Refer to Table 1 for identification of fossil localities. Shaded patterns in Tethys connects margins with shelfal carbonates that lack ammonoids.

we used a value for the solar constant of 1.370 × 10^3 W m^2 and the present orbital status of the Earth.

This simulation employs a seasonal model in which solar insolation varies throughout the year. The atmosphere is coupled thermally but not dynamically to a mixed layer ocean, 50 m deep, with a 5° × 5° surface grid (Washington and Meehl, 1984). The deeper ocean is external to the model. The lack of dynamic coupling has obvious repercussions on the overall transport and distribution of oceanic heat and atmospheric feedbacks. The sea surface temperature (SST) and sea ice extent are computed as a function of the surface energy balance. Sea ice forms when the SST falls below −1.8° C.

GCM's have been utilized to generate both annual and seasonal paleoclimate simulations for different geologic intervals, reconstructions, atmospheric concentrations of CO_2, and a variety of sensitivity tests. Pre-Pleistocene annual and seasonal simulations include the Eocene (Sloan, 1990; Sloan and Barron, 1988, 1989), mid-Cretaceous (Barron, 1985; Barron and Washington, 1984, 1985; Kruijs and Barron, 1990), Late Jurassic (Moore et al., 1992a), and Late Permian-Triassic (Kutzbach and Gallimore, 1989). We used biotopes and climatically sensitive lithotopes to test the sensitivity of the model results to the geologic record. Moore et al. (1992a) conclude that four times the pre-Industrial level of 280 ppm CO_2 (Barnola et al., 1987), 1120 ppm CO_2, is suitable for the Late Jurassic paleoatmosphere and yields results consistent with the geologic record. The majority of comparisons shows a remarkably positive correlation between the admittedly fragmentary geologic record and the model results. However, some provocative and some puzzling anomalies exist. Undoubtedly many result from the coarse nature of the CCM grid and the accuracy of input boundary conditions (paleogeography and paleotopography). However, some anomalies suggest that we may need to rethink previous interpretations or conclusions regarding the fossil record, particularly those of long-extinct forms.

The paleoclimate results are taken from a Late Jurassic simulation (Moore et al., 1992a). We utilize December/January/February (DJF) and June/July/August (JJA) seasonal paleoclimate maps of surface temperature (°C), sea ice distribution (m), precipitation–evaporation (mm d^{-1} both seasonal and annual) and wind-driven upwelling derived from the CCM wind stress data. With such paleoclimate information, factors other than paleogeography can be evaluated that could limit dispersal along coastlines or across seas. Limiting factors could be sea surface temperature (SST), changes related either to excess precipitation or evaporation, salinity, wind or oceanic circulation patterns, the presence or absence of upwelling, and a food chain.

Climate models have limitations. Among the realistic problems in present GCM's are the coarse nature of the land and sea grid cells, poorly controlled paleotopography, simplistic treatment of some parameters in part of the hydrologic cycle, and lack of dynamic atmospheric–oceanic coupling. Biostratigraphy can provide valuable feedback to model simulations and the lack of it has led to some misinterpretations.

LATE KIMMERIDGIAN AND TITHONIAN AMMONOIDS

Ammonoids were cephalopods that lived in shallow-to-moderate neritic depths (a few tens to a few hundred me-

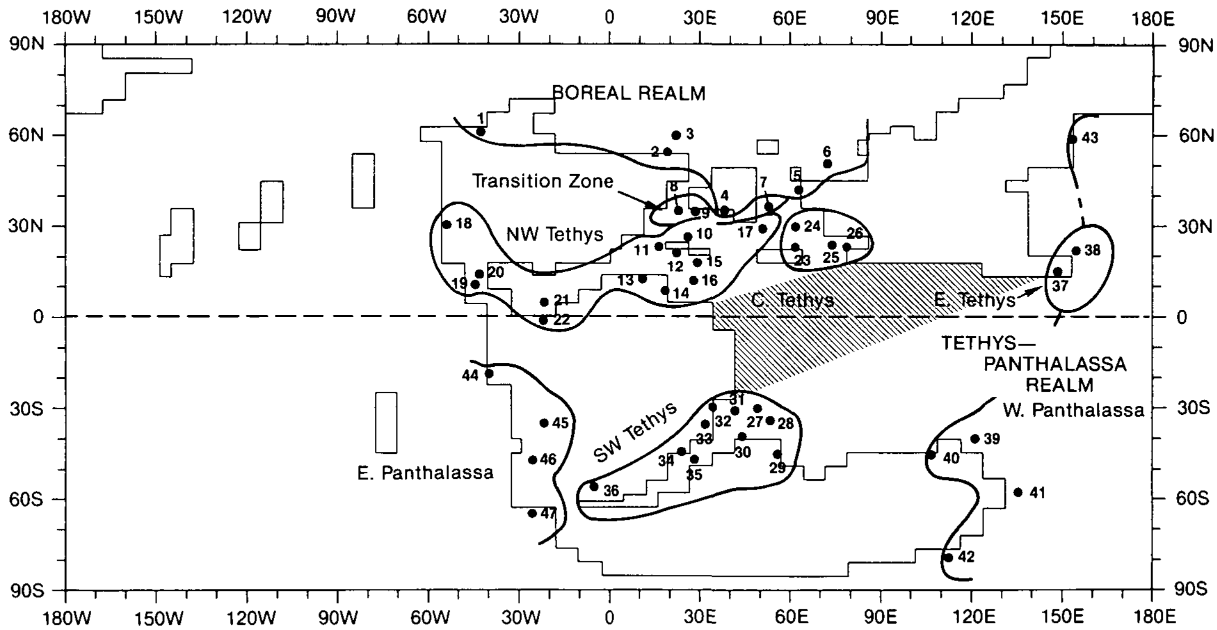

FIGURE 5—Distribution of ammonoid realms and provinces. See Table 2 for fossil localities by realm and province. Refer to Figure 4 for other details.

ters) and likely were predators of other neritic marine life, such as fishes, nudibranchs, and other cephalopods. In the Late Jurassic, the extensive continental margins and epeiric seas hosted a wide-ranging diverse ammonoid fauna. Ammonoids are reported from 47 localities or regions worldwide in the Kimmeridgian and Tithonian (Figs. 4 and 5; Table 1). The order Ammonoidea within this time interval changed from being very cosmopolitan to being strongly provincial.

TABLE 1—Kimmeridgian and Tithonian ammonoid localities. Compiled from Arkell et al., 1957.

1. N. Alaska	17. Crimea	33. Kenya
2. N. Greenland	18. California	34. Tanzania
3. Svalbard	19. Mexico	35. S. Madagascar
4. N. Germany – Poland	20. W. Texas	36. S. Africa
5. Russia	21. Cuba	37. Indonesia
6. W. Siberia	22. Trinidad	38. Borneo
7. S. Russia	23. Anatolia	39. New Guinea
8. England (London B.)	24. Caucasus	40. N. W. Australia
9. N. France	25. Kurdistan	41. New Caledonia
10. S. France	26. Persia	42. New Zealand
11. Spain	27. Pakistan	43. Japan
12. Balerics, Majorca	28. Salt Range	44. Peru
13. Algeria	29. Himalayas	45. Paraguay
14. Tunisia	30. Cutch	46. Argentina
15. Moravia and C. Europe	31. Somalia	47. Patagonia
16. S. Greece	32. Ethiopia	

Distribution of Ammonoid Lineages

By the beginning of the Tithonian, the great evolutionary expansion of Early and Middle Jurassic ammonoids was complete and many of the distinctive lineages were already extinct or greatly reduced in generic diversity and numbers (Fig. 6). In addition, during the Tithonian, the distribution of ammonoid faunas changed from being nearly cosmopolitan in the Middle Jurassic and early part of the Late Jurassic to being much more provincial. This provinciality is associated with the development of new lineages at the subfamily level from a few conservative long ranging groups (Fig. 6). Many of the new lineages, as well as several of the conservative lineages, continued into the Early Cretaceous where they formed the stocks from which Cretaceous ammonoids radiated.

Tithonian members of the suborder Phylloceratina, the single stem group surviving from the Triassic and from which other Jurassic ammonoids evolved, were reduced to only five genera which belonged in two subfamilies of the family Phylloceratidae. These five genera were all relatively slowly evolving, long ranging, and widely distributed. Typically they had thin shells, minor linear ornamentations, and minor, if any, shell constrictions. Although rare in the Boreal Realm, they were worldwide in distribution and were generally an abundant part of many Tithonian ammonoid assemblages. Little paleobiogeographic significance can be attributed to distributions within this suborder. Their wide distribution hints at their being adapted to deeper, cooler shelf and open-ocean waters from where they may have given rise to a number of lineages that periodically adapted to shallower, warmer water shelves.

The suborder Lytoceratina during the Tithonian also was a small group totalling seven genera in only three families (Fig. 6). These evolute to loosely coiled shells had rounded whorls and many had flared apertures. In contrast

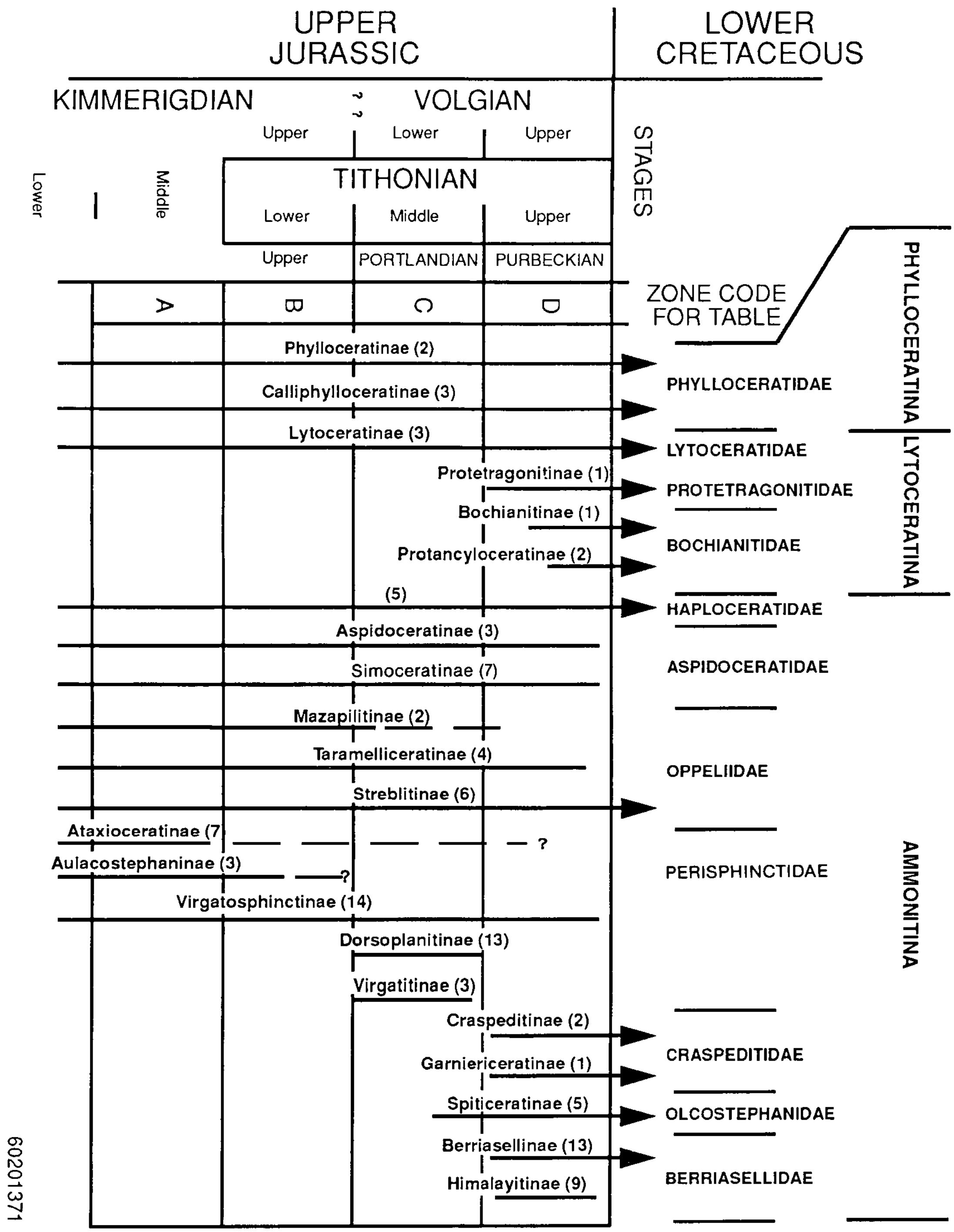

FIGURE 6—Chart showing ordination, range, and extinction of Kimmeridgian and Tithonian ammonoid subfamily lineages and generic numbers in each.

to many other ammonoids, they had a single leathery apertural covering (an anaptychus). Most Jurassic Lytoceratina families became extinct before the Kimmeridgian so that in the Tithonian two of the three families were actually part of a new, very late Jurassic diversification that formed lineages which became important in the Cretaceous. The main lineage, the family Lytoceratidae, had very evolute shells and was widespread and morphologically conservative. The family Protetragonitidae first appeared in the upper part of the Tithonian with only one genus and it had a northwestern to central Tethyan distribution. The Bochianitidae also first appeared in the upper part of the Tithonian and it was represented by only three genera.

The most diverse of the Tithonian ammonoids was the suborder Ammonitina which included seven families and fifteen subfamilies (Fig. 6). The families Aspidoceratidae, Haploceratidae, Oppeliidae, and Perisphinctidae were long-ranging and extended into the Tithonian from much earlier in the Jurassic. Arkell et al. (1957) considered the Aspidoceratidae to be polyphyletic, developing as a series of specializations from various parts of the Perisphinctidae at different times in the Late Jurassic. The geographic distribution of individual genera hints at such origins because their phylogeny is poorly understood and their distribution is difficult to interpret. The Aspidoceratinae, like their supposed perisphinctid ancestors, were widely distributed in the northwest and central parts of the Tethys during the Tithonian. On the other hand, the other subfamily, the Simoceratinae, was known mainly from the Southwest Tethys and West Panthalassa provinces.

The family Oppeliidae (Fig. 6) had compressed to oxycone shells that were unkeeled to multiple-keeled with falcoid to falcate ribbing. The three Tithonian subfamilies were those that survived from earlier in the Jurassic and, of these, only the Streblitinae persisted into the Cretaceous. The Taramelliceratinae with ornate shells and prominent ribs was the most common subfamily and the most widespread. The Streblitinae were restricted to the Southwest Tethys Province and the Mazapilitinae to the Northwest Tethys and/or East Panthalassa provinces.

The family Haploceratidae was a group of small, smooth-shelled, typically unkeeled and unribbed ammonitines with wide Tethyan distributions. Arkell et al. (1957) favored the idea that this family was also polyphyletic and that its Tithonian genera probably evolved at different times from the Phylloceratina. During the Tithonian, genera in this family were typically northwestern and southwestern Tethyan in distribution.

A much more rapidly evolving set of Tithonian lineages was present in the Perisphinctidae and its related family, the Craspeditidae (Fig. 6). The subfamilies Ataxioceratinae and Aulacostephaninae ranged into the Kimmeridgian from earlier in the Jurassic but became rare before the end of that stage. They were basically Tethyan in distribution. Two genera of Ataxioceratinae locally may have ranged into the upper Tithonian. Foremost among the perisphinctids was the subfamily Virgatosphinctinae which had relatively long ranging genera through the Kimmeridgian and Tithonian. Many of these genera were widely distributed. In the Tithonian, this subfamily was particularly important in the Central and Southwest Tethys provinces.

Two other perisphinctid subfamilies were confined to the Boreal Realm. One of these, the Dorsoplanitinae, were giants of Portlandian age and had evolute, rounded whorl, strongly ribbed shell with simple sutures. They extended from Greenland, through England, Russia and into central Siberia. Arkell et al. (1957) considered other reported occurrences questionable. Our paleoclimatic studies suggest that in the Boreal Realm cold surface, particularly shelf water temperatures and current directions may have been important in controlling their distribution. The other Boreal subfamily is the Virgatitinae which consists of three genera that clearly identify the lower part of the provincial Russian Volgian Stage (Fig. 6). These are relatively large specimens with strongly developed ribbing. Commonly as many as six or seven secondary ribs arose from a single primary rib.

Three specialized families, the Craspeditidae, Olcostephanidae, and Berriasellidae (Fig. 6) were all known only from the upper part of the Tithonian. Of these, the Craspeditinae were involute planulates with platycone and oxycone shells that showed a loss of ribbing. Arkell et al. (1957) believed this family was derived from the Dorsoplanitinae. It was endemic to the Volgian province during the late Tithonian.

The early olcostephanid subfamily Spiticeratinae had planulate shells with umbilical tubercles, bundled ribs, and strong shell constrictions. Its origins are not well understood. Its Tithonian distribution was in the Northwest, Central, and Southwest Tethys provinces.

The most diverse family of late Tithonian Ammonitina was the Berriasellidae which was typically planulate. This group continued into the Cretaceous where it was very important. During the Tithonian the subfamily Berriasellinae was widely distributed in the Tethyan and Panthalassan realms. It was common in the East Tethys and West Panthalassa provinces. In contrast, the subfamily Himalayitinae had three groups of genera. One group of genera was found mainly in the East Panthalassa; another was common in the Central and Southwest Tethys; and the third group was common in the Central and Southwest Tethys and East Panthalassa provinces.

Tithonian Provinces

Arkell (1956) and Enay (1973) recognized that Tithonian ammonoids were distributed in two broad faunal realms. We have reexamined these faunal realms using Arkell's geographic distributions of Tithonian ammonoids (Table 2; Fig. 5) and compared them with our paleoclimate models using Late Jurassic paleogeographic reconstructions. Among the ammonoids, only the family Phylloceratidae and the lytoceratid genus *Lytoceras* are considered cosmopolitan.

Boreal Realm

During the middle Kimmeridgian, the area that became the Boreal Realm had only a few, widespread genera of Simocertinae, Ataxioceratinae, and Aulacostephaninae. The low diversity of this assemblage could be interpreted as the response by a warm adapted fauna to cooler water.

Of the Tithonian ammonoid biogeographical areas, the Boreal Realm is the most clearly defined partly because the faunas had a very low generic diversity and partly

TABLE 2—Distribution of Kimmeridgian and Tithonian ammonoid genera by realm and province. Compiled from Arkell et al. (1957) and Enay (1973).

GEOGRAPHICAL DISTRIBUTION			BOREAL REALM						TRANS			TETHYS-PANTHALASSA REALM																																					
												TETHYS SUBREALM																												PANTHALASSA SUBREALM								
												NORTHWEST													CENTRAL				SOUTHWEST										EAST		WEST					EAST			
FAMILY/SUBF.	GENERA	ZONE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
PHYLLOCERATIDAE																																																	
Phylloceratinae																																																	
	Phylloceras	A-D	WORLDWIDE DISTRIBUTIONS																																												
	Partschiceras	A-D	WORLDWIDE DISTRIBUTIONS																																												
Calliphylloceratinae																																																	
	Calliphylloceras	A-D	WORLDWIDE DISTRIBUTIONS																																												
	Holcophylloceras	A-D	WORLDWIDE DISTRIBUTIONS																																												
	Ptychophylloceras	A-D	PROBABLY WORLDWIDE DISTRIBUTIONS																																												
LYTOCERATIDAE																																																	
Lytoceratinae																																																	
	Lytoceras	A-D	WORLDWIDE DISTRIBUTION																																												
	Hemilytoceras	A-D										X			X	X	X																	X																	
	Pterolytoceras	B-D?																													X	X																		
PROTETRAGONITIDAE																																																	
	Protetragonites	D									X	X																																					
BOCHIANITIDAE																																																	
Bochianitinae																																																	
	Bochianites	D										?			X	X				X	X											X						X	X										
Protancyloceratinae																																																	
	Protancyloceras	D										X			X	X	X		X		X		X					X	X																		X			
	Cochlorioceras	D																										X																						
HAPLOCERATIDAE																																																	
	Haploceras	A-D								X	X	X	X	X	X	X					X	X	X				X					X				X	X												
	Pseudolissoceras	D										X				?					X		X				X																					X	
	Neolissoceras	D										X																		X							X												
	Hildoglochiceras	B-D																			X		X		X						X	X				X	X												
	Glochiceras	B-D							X	X	X	X									X		X				X					X	X			X									X			X	
ASPIDOCERATIDAE																																																	
Aspidoceratinae																																																	
	Aspidoceras	A-B							X	X	X	X			X	X			X		X	X	X									X		X	X	X	X							X	X			X	
	Orthaspidoceras	A								X	X	X																					X				X												
	Physodoceras	A							X	X	X	X									X	X	X								X	X		X	X		X												
Simoceratinae																																																	
	Virgatosimoceras	A				X						X											X					X					X																
	?Lytogyroceras	A-D										X																																					
	Hemisimoceras	A																																			X												
	Pseudoclambites	B-D?																															X																
	Aulasimoceras	B-D				?									X	X																																	
	Hybonoticeras	B										X			X	X					X		X		X							X	X	X	X	X	X												
	Simoceras	B-D										X	?	X	X	X							X			X		X					?															X	
OPPELIIDAE																																																	
Mazapilitinae																																																	
	Mazalities	B-D																			X																												
	Eurynoticeras	A-B										X																																					
Taramelliceratinae																																																	

TABLE 2—Continued.

GEOGRAPHICAL DISTRIBUTION			BOREAL REALM						TRANS			TETHYS-PANTHALASSA REALM																																					
												TETHYS SUBREALM																													PANTHALASSA SUBREALM								
												NORTHWEST													CENTRAL				SOUTHWEST										EAST		WEST					EAST			
FAMILY/SUBF.	GENERA	ZONE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
	Taramelliceras	A-D?								X	X	X			X	X					X							X			X	X			X	X	X		X						X				
	Fontannesiella	A-D?									X	X																																					
	Metahaploceras	A-D?								X	X	X									X		X									X					X												
	Hemihaploceras	A-D?										X																				X																	
Streblitinae																																																	
	Uhligites	B-D																			X				X						?	X			X		X		X										
	Gymnodiscoceras	B-D?															X																																
	Substreblites	B-D										X					X		X																														
	Semiformiceras	B-D															X																																
	Cyrtosiceras	B-D										X					X		X																														
	Oxylenticeras	B-D										X															X																						
PERISPHINCTIDAE																																																	
Ataxioceratinae																																																	
	Lithacocera	A			X					X	X	X														X						X			X		X								X			X	
	Virgataxioceras	A				X			X												X												X																
	Kossmatia	D								X	X	X			X	X				X	X	X			X	X	X	X			X								X		X	X		X		?	?	?	
	Paraboliceras	A-D																							X	X	X	X			X								X					X					
	Parabolicertoides	A-D																									X	X			X																		
	Procraspedites	A																			X																												
Aulacostephaninae																																																	
	Gravesia	A								X	X	X																									?												
	Enosphinctes	A				X				X	X	X																																					
	?Simocosmoceras	A								X	X	X																																					
Virgatosphinctinae																																																	
	Subdichotomoceras	A, B?		?						X											?										X	X	X		X	X	X												
	Torquatisphinctes	A-B, C?							X												X											X	X		X		X											X	
	Katroliceas	B, C?										X	X	X																		X	X		X		X								X				
	Metagravesia	B																														X																	
	Subdichotomoceras	B-C, D?		?								X	X	X							?										X	X	X		X	X	X												
	Aulacosphinctoides	B-C																			X							X			X	X	X		X	X	?							X	X			X	
	Parapallasiceras	B				?																											X																
	Subplanites	A-B		?					X	X	X	X									X											X	X	X						X									
	Anavirgatites	A-B								X	X	X						?															X																
	Pseudovirgatites	B-D				X											X																?																
	Djurjuriceras	B										X	X	X	X	X																																	
	Pectinatites	B		X					X	X	X	X									?																											?	
	Paraberriasella	B										X																																					
	Wheatleyites	B							X	X											?																												
	Sublithacoceras	B				X						X			X																		X																
	Virgatosphinctes	B-D											X								X		X	X	?	X		X	X		X	X		?		X	X					X						X	
	Pseudoinvoluticeras	B-D																			X		X		X								X	?	X	X	X											X	
	Phanerostephanus	B-D											X												X		X										X												
	Nothostephanus	B-D																									X																						
	?Nannostephanus	B-D										X															X																						
Dorsoplanitinae																																																	
	Pavlovia	C		X			X	X		X	X																																					?	
	Paravirgatites	C		?						X	X																																						
	Epipallasiceras	C		X																																													

TABLE 2—Continued.

GEOGRAPHICAL DISTRIBUTION			BOREAL REALM						TRANS			TETHYS-PANTHALASSA REALM																																				
											TETHYS SUBREALM																												PANTHALASSA SUBREALM							
											NORTHWEST												CENTRAL				SOUTHWEST										EAST		WEST					EAST			
FAMILY/SUBF.	GENERA	ZONE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
	Dorsoplanites	C		X	X		X	X		?															?						?																		
	Laugeites	C		X			X	X																																										
	Epivirgatites	C					X																																											
	Lomonossovella	C					X																																											
	Acuticostites	C					X																																											
	Glaucolithites	C		X						X	X																																							
	Titanites	C		?			X			X	X															X																								
	Kerberites	C					X			X	X																																							
	Glottoptychinites	C								X																																								
	?Simotoichites	C								X																																								
Virgatitinae																																																
	Zaraiskites	C				X	X			X																																								
	Virgatites	C					X																																											
	Michalskia	C					X																																											
CRASPEDITIDAE																																																
Craspiditinae																																																
	Craspedites	D		X			X																																											
	Kachpurites	D					X																																											
Garniericeratinae																																																
	Garniericeras	D					X																																											
OLCOSTEPHANIDAE																																																
Spiticeratinae																																																
	Proniceras	B-D										X	X	X	X	X	X				X				X	X			X								X												
	Umiates	B-D										X	X	X	X	X																	X					X												
	Spiticeras	D										X			X	?	X				X		X						X		X						X											X	
	?Bihenduloceras	B-D?																																	X														
	?Aspidostephanus	B-D?										X		X	X	X																															X	
BERRIASELLIDAE																																																
Berriasellinae																																																
	Berriasella	B-D								X	X	X	X	X	X	X			X	X	X		X		X	X	X	X			X						X						X	X				X	X
	Dalmasiceras	D								X	X	X				X																																
	Substeueroceras	D																	X	X						X	X					?														X		X	
	Protacanthodiscus	B-D										X	X	X	X	X			X	X	X						X			X	X																X		X	
	Lytohoplites	B-D												X								X							X							X									X		X	
	Raimondiceras	B-D?																												X																X			
	Andiceras	B-D																																														X		
	Riasanites	D					X														?				?																							?		
	Blanfordiceras	D?																							X		X	X		X	X								X		X		X								X	X
	Pseudoargentiniceras	D								X	X	X			X	X															?																		
	Protothurmannia	B-D																			X																												
	Parodontoceras	D																		?	X		X				X						?												X		X	
	?Somaliceras	B-D?																																?															
Himalayitinae																																																
	Hemispiticeras	D																																														X	
	Dickersonia	B-D																						X																									
	Windhauseniceras	B-D																																														X	
	Corongoceras	B-D												X						X		X																									X	X
	?Aulacosphinctes	B-D												X					?												X	X	X	?			X										X		X	
	Himalayites	B-D									X				X	X					X										X	X						X		X							X		X	
	Micracanthoceras	B-D										X			X						X		X							X				X	X														X	
	Durangites	B-D										X			X	X				X	X		X																									
	Tithopelloceras	B-D										X	?	X	X	X		X																														

because they became so strongly endemic during this time. In the early Tithonian, the Boreal Realm was characterized by a low generic diversity that includes a few genera that belonged mainly to the perisphinctid subfamily Virgatosphinctinae. These genera included a number of endemic species lineages which in turn gave rise to later ammonoids in this area. By middle Tithonian, the Boreal Realm was the home to an almost entire endemic set of genera that made up the perisphinctid subfamily Dorsoplanitinae. Boreal Realm endemism continued into the late Tithonian with the endemic peripshinctid subfamily Virgatitinae and the endemic family Craspeditidae. In addition, the late Tithonian Boreal Realm includes a single genus from the Berriasellidae, *Riasanites,* and one genus in the Aspidoceratidae, *Virgatosimoceras.*

The faunas of the Boreal Realm (Table 2, columns 1–6) have been considered low diversity, cool to cold water adapted faunas that were climatically isolated. Comparison with our paleoclimate reconstructions supports that interpretation. Because of their strongly endemic ammonoid faunas and the associated difficulties of correlating these faunas with ammonoid zones of the Tethys, the middle and late Tithonian deposits of the Boreal Realm are also referred to as the Volgian Stage.

Transition Zone

A few typically Boreal genera appeared in a narrow latitudinal belt across western, central and eastern Europe just south of the Boreal Realm in what was a well defined Transition Zone with ammonoid faunas typical of the Northwestern Tethys (Table 2, columns 7–9). One Boreal genus, *Titanites,* also occurs in Crimea at the northern shores of the Tethys. This Transition Zone includes a few genera not recorded from either the typical Boreal or typical Tethys ammonoid assemblages, such as *Subdichotomoceras, Glottoptychinites,* and probably *Simotoichites* and *Paravirgatites.*

The middle Kimmeridgian and early Tithonian ammonoid genera of the Transition Zone had mostly Tethys affinities. During the middle Tithonian, it had a relatively large number of genera belonging to the typically Boreal subfamily Dorsoplanitinae. By the late Tithonian, however, the Transition Zone lacked the Boreal Craspeditidae and was clearly made up of two cooler water arms of the Northwestern Tethys, based on low generic diversity of typically Tethys genera. This Transition Zone reflects the important, strong ecological gradients that must have separated the two major realms.

Tethys-Panthalassa Realm

In contrast to the Boreal Realm, the Tethys-Panthalassa Realm (Table 2, columns 10–47) contained a much more abundant and diversified ammonoid fauna in which the families Bochianitidae, Haploceratidae, Aspidoceratidae, Olcostephanidae, and Berriasellidae were widely distributed. Within the Perisphinctidae, the subfamilies Ataxioceratinae, Aulacostephaninae, and Virgatosphinctinae were particularly important and largely restricted to the Tethys-Panthalassa Realm. This realm has been interpreted as being characterized by a warm- to tropical-water adapted ammonoid fauna. Again, comparison with climatic modeling on our late Jurassic paleogeographic reconstruction supports that interpretation.

This realm is divisible into two subregions, a Tethys Subrealm (Table 2, columns 10–38) and a Panthalassa Subrealm (columns 39–47), based on differences in generic diversity and in the distribution of the dominant subfamilies and genera.

The Tethys Subrealm was the area of major ammonoid diversity during the Tithonian. In addition to the cosmopolitan genera of Phyllocedratidae and the lytoceratid genus *Lytoceras,* nearly all subfamilies of the ammonoids are well represented. Only the perisphinctid Aulacostephaninae (basically a Transition Zone subfamily), the Dorsoplanitinae and Virgatitinae (Boreal subfamilies) and the Crespeditidae (a Boreal family) were either not present, very rare, or their few occurrences are questioned. The Tethys Subrealm can be subdivided into four provinces based on the dominance of genera in different families and subfamilies. A few diagnostic genera were apparently restricted to particular provinces.

The northwestern branch of the Tethys (Table 2, columns 10–22) was dominated by genera of Olcostephanidae and Berriasellidae. In these families, the genera *Pseudoargentiniceras, Dalmasiceras, Protothurmannia, Dickersonia, Corongoceras* (which in the Late Tithonian dispersed into the Eastern Panthalassa Province), *Durangites,* and *Tithopeltoceras* were characteristic of this Northwestern Tethys Province. Also *Djurjuriceras,* a virgatosphinctine perisphinctid, is confined to this province.

A Central Tethys Province composed of parts of Turkey (Anatolia), Caucasus, Kurdistan, and Persia, and perhaps Pakistan, was characterized by having relatively common occurrences of the perisphinctid ataxioceratine genera *Kossmatia, Paraboliceras,* and *Parabolicertoides.* These localities had few virgatosphinctine genera in common with the Southeastern Tethys Province and apparently lacked the berriasellid Himalayitinae. This Province also lacked many of the early and middle Tithonian Olcostephanidae genera that were common in the Northwestern Tethys Province. Only rare bochianitid *Cochlorioceras* and rare virgatosphinctine *Nothostephanus* appear to be endemic to this province. It shares the berriasellid *Blanfordiceras* with the provinces to the southwest and to the east, and shares the bachianitid *Protancyloceras* and most of the genera of Streblitinae with the Northwestern Tethys Province.

It appears significant that the Central Tethys Province had a relatively low generic diversity compared to both the Northwestern and Southwestern Tethys provinces. It was closest to the large area in the Arabian Peninsula and northcentral and northeastern Africa that lacks ammonoids of Tithonian age. This area that lacks ammonoids is shown on our paleoclimate maps as an area of high

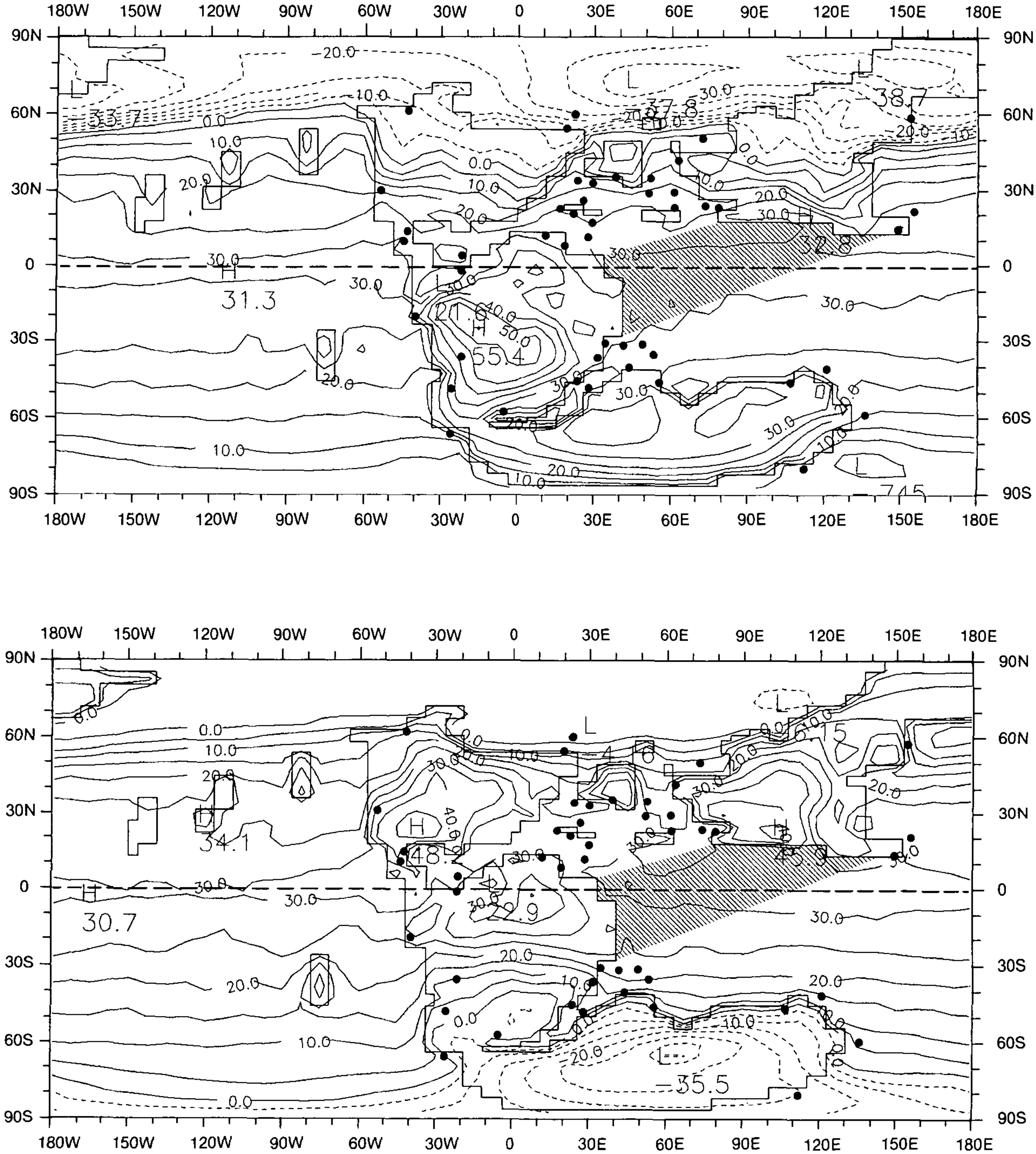

FIGURE 7—Dec/Jan/Feb (top) and June/July/Aug (bottom) Kimmeridgian and Tithonian surface temperature (°C) distribution using 1120 ppm CO_2 simulation with ammonoid localities. See Figure 4 for explanation.

evaporation and high temperatures and, therefore, was likely an area with elevated surface water salinities which was ecologically not suited for ammonoids. The southwestern arm of the Tethys, on the other hand, was dominated by a large number of perisphinctid virgatosphinctine genera, although only a few of these genera were restricted geographically to this Southeastern Tethys Province. Those genera apparently restricted to this province include *Metagravesia*, *Parapallasiceras*, and *Nothostephanus*. In addition, the olcostephanid *Bihenduloceras* is questionably identified only in this province from one locality. The berriasellid *Raimondiceras* is rare in this and the East Panthalassa Province in the late Tithonian.

The fourth Tethys ammonoid province of Tithonian age

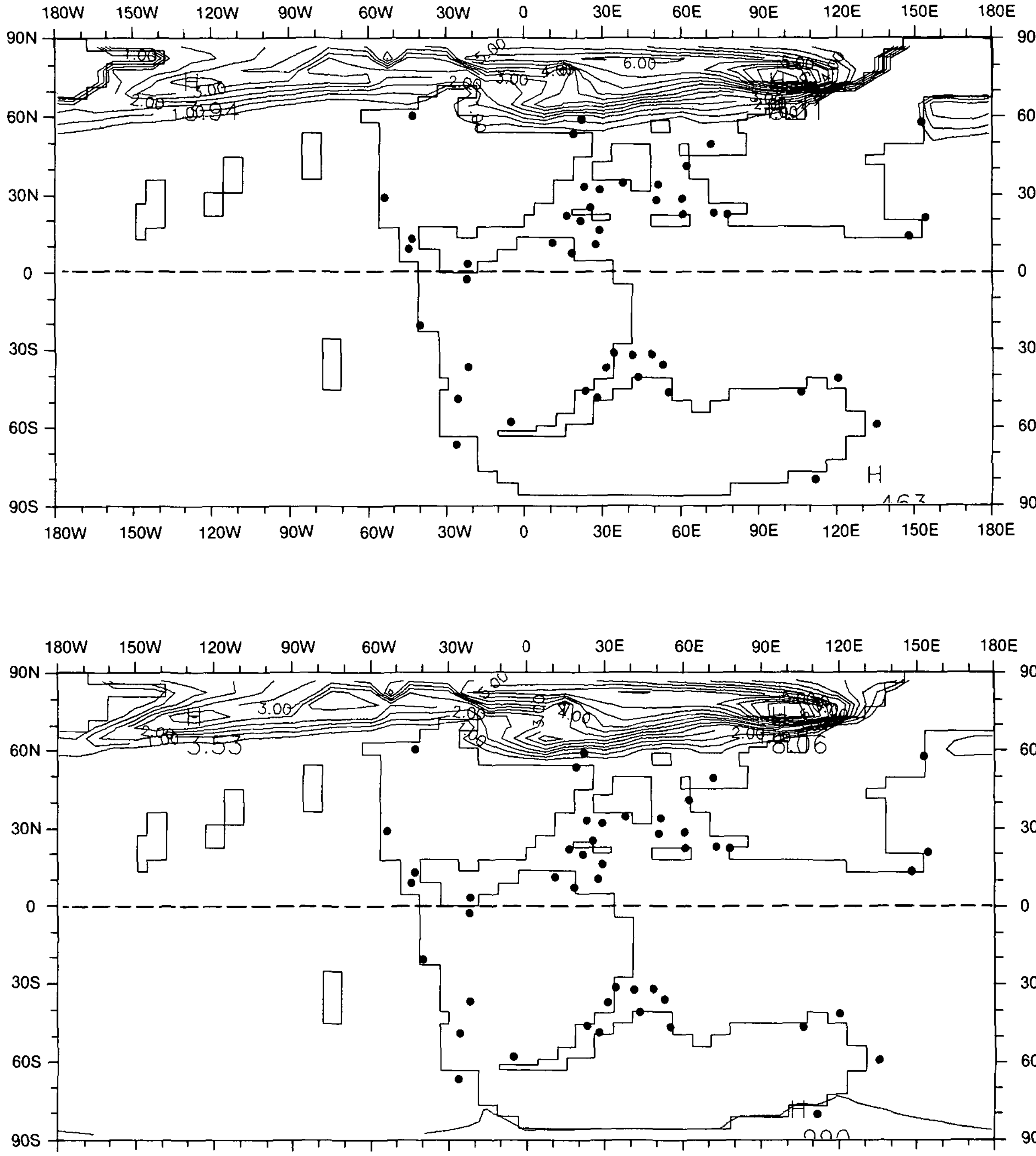

FIGURE 8—Dec/Jan/Feb (top) and June/July/Aug (bottom) Kimmeridgian and Tithonian sea ice (m) distribution using 1120 ppm CO_2 simulation with ammonoid localities. See Figure 4 for explanation.

was located in Borneo and Indonesia. This Eastern Tethys Province is known from a small number of localities from which only eight genera are reported. It may have been an eastward extension of the Southwestern Tethys Province across the shelf areas of the northern Australian part of Gondwana, because all eight genera also occur in that Province. Five of the eight genera also occur in the Panthalassa Subrealm. Although the low generic diversity suggests that the Eastern Tethys Province was ecologically poorly suited for most of the typical Tethys ammonoid genera, it is also possible that Tithonian ammonoids in the region are incompletely collected and the fauna represents a transition zone between the Tethys and Panthalassa subrealms.

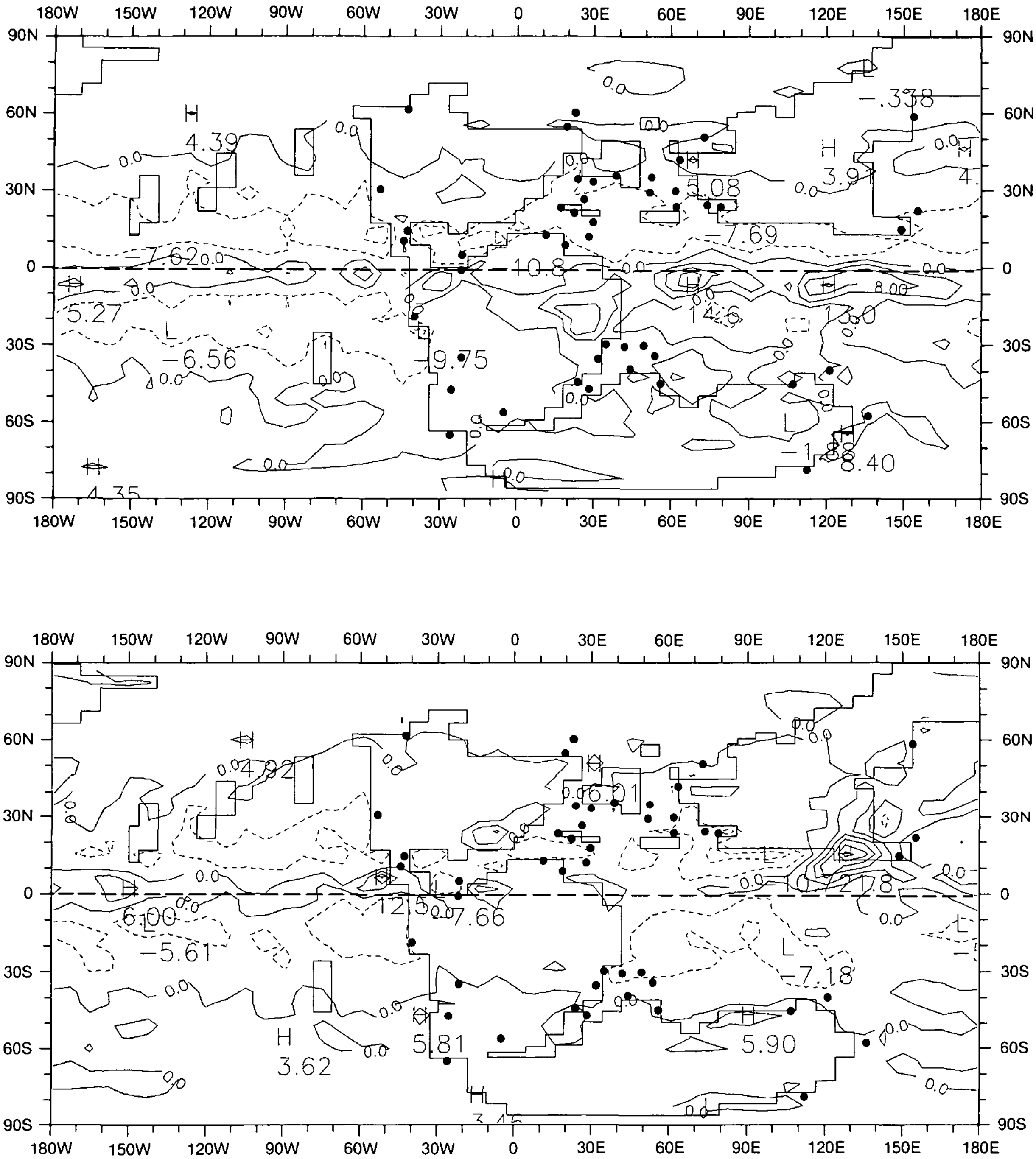

FIGURE 9—Dec/Jan/Feb (top) and June/July/Aug (bottom) maps of Kimmeridgian and Tithonian precipitation–evaporation (P-E) in mm d^{-1} with ammonoid localities. Solid lines = net precipitation; dashed lines = net evaporation. See Figure 4 for explanation.

The Panthalassa Subrealm in the late Kimmeridgian and early Tithonian included a few genera of Perisphinctidae, but only a handful of other genera. However, by the middle and late Tithonian, it had mostly genera belonging to the Olcostephanidae and Berriasellidae in its Eastern Province. Many of these genera dispersed into the Eastern Panthalassa Province from the southwest through a newly opened seaway around southern Africa-South America and through the Caribbean end of the Northwestern arm of the Tethys. These dispersals resulted in a late Tithonian Eastern Panthalassa Province that was very rich in northwestern Tethys and Southwestern Tethys genera and formed a faunal continuum that almost encircled the Africa-South America continent.

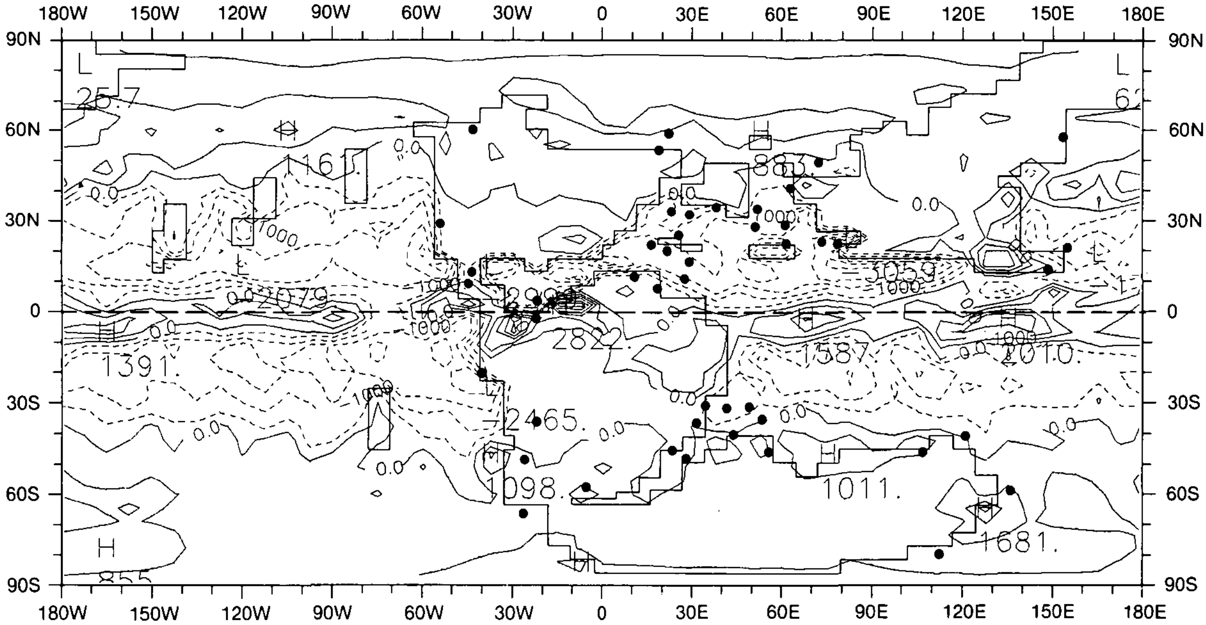

FIGURE 10—Map of annual Kimmeridgian and Tithonian precipitation–evaporation (P-E) in mm yr^{-1} with ammonoid localities. Solid lines = net precipitation; dashed lines = net evaporation. See Figure 4 for explanation.

In the Western Panthalassa Province, early Tithonian faunas are known from accreted terranes and rafted blocks and include only eight widespread Tethys genera. By the late Tithonian this province had only two genera of Berriasellidae, and a single, widespread genus, *Kossmatia*, of Perisphinctidae.

Our analysis of the ammonoid distribution shows that the initial simulated reconstruction of the paleogeography (Fig. 2) placed New Zealand at a high southern latitude (Stevens, 1989; Scotese, 1991; and Rowley, 1992). However, our faunal argument is sufficiently reasonable to postulate that certain parts of these tectonically complex islands, which were subtropical to tropical in the Late Permian (Ross and Ross, 1983), were probably tropical in the Late Jurassic also. As the Kimmeridgian simulation was run using the reconstruction in Figures 2 and 3, the paleoclimate maps carry that landmass configuration.

PALEOCLIMATE AND AMMONOID PROVINCES

In portions of the central Tethys Sea where normal marine shelfal carbonates exist ammonoid faunas (Arkell, 1956; Arkell et al., 1957; and Enay, 1973) are absent (Fig. 4, Table 2) along the northern margin of the Tethys, from eastern Turkey to Indonesia, and also along the western margin, from Libya through Saudi Arabia. These two areas outline the equatorial part of the Tethys Sea (Fig. 4). By late Tithonian time, additional narrow seaways connected the Tethys with the other oceans. However, even with these narrow and probably shallow connections, the Tethys was dominated by equatorial to subtropical paleoclimates. In the following paleoclimatological maps (Figs. 8 to 12), faunal localities are shown for reference.

The SST exceeds 30° C in both seasons throughout the equatorial Tethys Sea and Panthalassa Ocean (Fig. 7). These margins also are largely devoid of ammonoid localities as observed by Enay (1973). From this relationship, we infer that tropical ammonoids were limited by SST that exceeded 30° C, or even possibly less. Saunders and Spinosa (1979) and Saunders (1984) noted that 25° C appears to be an upper limit for present-day *Nautilus*. As the Tethys was largely isolated from cold high latitude water, the entire neritic zone may have had temperatures similar to the SST. Further, Ward (1987) argues that Mesozoic nautiloids lived in deeper water than ammonoids. If ammonoids occupied the shallower part of the neritic zone, they would be more affected by the ambient SST. We believe this gives confidence to the CCM modeled tropical SST of the Tethys Sea and serves to help calibrate this simulation. High temperature was also a barrier to the distribution and dispersal of ammonoids. About 85% of all ammonoid localities had seasonal SST of 20° C or higher. From this we suggest SST favoring ammonoid expansion lay in the range of 20° to less than 30° C.

Seven localities lay in regions where the summer SST are in the 20° to 5° C range (Fig. 7). Two localities occur in regions where sea ice forms in the DJF and JJA respective hemisphere winter seasons (Fig. 8). Another paleoecologic characteristic appears to suggest that the high latitude boreal and austral forms could survive in cold SST and at two localities, at least, could possibly winter under sea ice.

An important measure of the hydrologic cycle is, whether over a given interval, precipitation exceeds evaporation or vice versa. In this discussion, such calculations of precipitation minus evaporation and resulting maps are re-

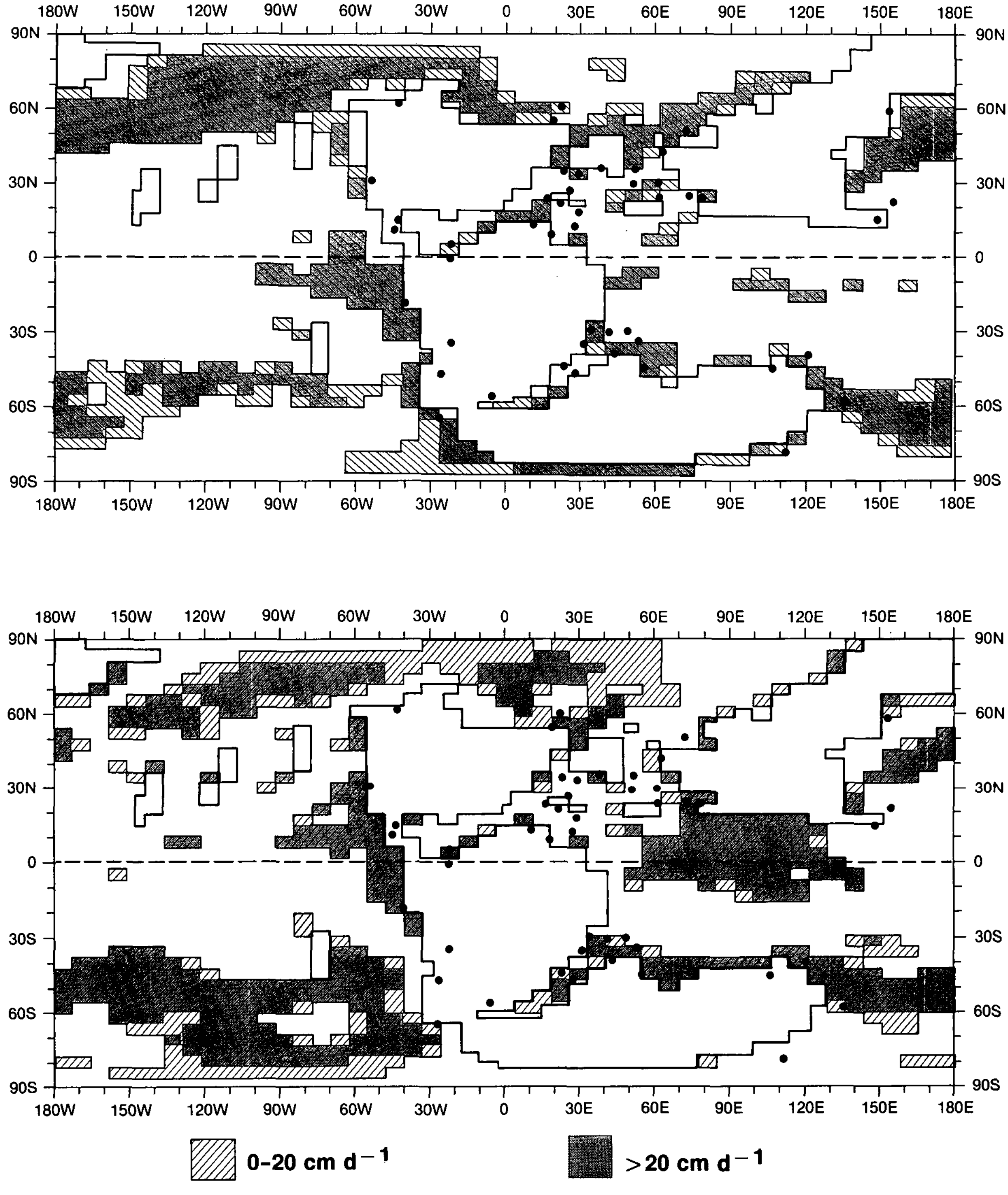

FIGURE 11—Dec/Jan/Feb (top) and Jan/July/Aug (bottom) Kimmeridgian and Tithonian wind driven upwelling with overprint of ammonoid localities.

ferred to as "P-E." For this study we show the DJF, JJA, and annual P-E maps for the modeled interval (Figs. 9, 10). The maps are important for this study because they show net precipitation (solid lines; positive P-E) or net evaporation (dashed lines; negative P-E). From these relationships we can infer respectively, oceanic salinities that are either lower or higher than normal.

In DJF, a nearly continuous band of net precipitation exists between 0° and 10° S. The JJA precipitation band is weak and occurs only in the Panthalassa Ocean. It terminates westward in a monsoon-dominated, focused center of rainfall over southeast Gondwana (Moore et al., 1992a). The annual P-E map (Fig. 10) has a pattern similar to the DJF season (Fig. 9). Ammonoid localities lie on either side of these net precipitation belts. The majority of localities occur in regions with net evaporation. Those poleward of 50° latitude are in oceans with a slightly positive P-E (Fig. 10).

The ammonoid gap on the western margin of the Tethys coincides largely with one of net precipitation (Fig. 10). However, in the JJA season it is weakly evaporative. In contrast, the northern Tethys margin ammonoid gap is evaporative in both seasons, and a strong annual focus of evaporation. This would suggest that a negative, or at most slightly positive, P-E is a favorable paleoecological factor; however, it does not appear to dominate over others, such as SST.

Wind-driven, coastal upwelling has been shown to correlate with high primary biologic productivity in the present World Ocean and the mid-Cretaceous ocean (Kruijs, 1989; Kruijs and Barron, 1990). High biologic productivity is the basis for the highly organic productive regions of the ocean and presumably was so in past geologic intervals, at least during the Mesozoic and Cenozoic eras. Comparison of wind-driven, coastal upwelling in both seasons with the reported localities of Kimmeridgian and Tithonian ammonoids shows that 39 of the 47 localities (85%) are found where upwelling occurs in at least one season and 24 localities (63%) where upwelling occurs in both seasons (Fig. 11, Table 3). We interpret the strongly positive correlation of wind-driven seasonal upwelling and ammonoid localities to reflect abundant faunas in nutrient-rich environments.

The two areas of the Tethys lacking ammonoids show apparently conflicting patterns. Easterlies in the DJF season produce no coastal upwelling along the northern Tethys margin and very restricted upwelling on the western Tethys margin (Fig. 11). The JJA wind reversal related to monsoonal circulation produces a vast region of intense upwelling in the north-central Tethys Sea. The lack of ammonoids here may reflect other factors. Ammonoids may have preferred seas with clear water and the associated fauna in contrast to seas with large volumes of terrestrial debris related to the heavy monsoonal and orographically forced precipitation and large amounts of sediment-rich runoff (Moore et al., 1992a).

Ammonoid Localities and Modeled Storm Tracks—Possible Tempestite Accumulations?

In this section we offer some speculations regarding certain ammonoid localities. At the outset, we want to emphasize that we have not investigated certain sites that lie in storm track paths (Figs. 12 and 13). Neither are we proposing nor implying that any one particular locality is a tempestite. We only want to point out to ammonoid experts and field geologists that if any assemblage in these areas appears chaotic or unusual, it is quite possibly storm-related.

TABLE 3—Comparison of ammonoid localities* with wind driven coastal upwelling for the four seasons.

Upwelling	Number of Localities	Percentage of Localities
Two or more seasons of Intense or Weak	29	63
One season of Intense	31	67
One season of Intense or Weak	39	85
No upwelling	7	15

Those localities on a land grid cell but adjacent to an ocean grid cell are counted as being in that ocean cell.

* Locality 45 is more than one grid cell from an ocean cell and is not included in these calculations.

Two major types of storm systems that can affect neritic and shoreline sedimentary deposits in the geologic record are low latitude cyclones and mid-latitude winter storms associated with the polar front. Information on such storms can be deduced from GCM paleoclimate simulation results (Barron, 1989). Cyclones form over the low latitude oceans where the SST exceeds 27° C (Fig. 7). The storms move in a generally zonal path and then into subtropical latitudes in response to variations in the sea level pressure gradient associated with the subtropical high. The upper level atmospheric wind stress can be used to drive a software program to predict mid-latitude winter storm tracks (Barron, 1989). Both sets of storms, if they make landfall, can leave evidence in the sedimentary record (Barron, 1989). Currently these storm systems possess a definite pattern of making landfall on rather restricted portions of the world's coastlines. We would argue that similar relationships existed in the geologic past. Thus, storm landfalls and related deposits can be repetitive in the rock column at certain localities. The Late Jurassic storm patterns are detailed in Moore et al. (1992a).

Cyclones moving through tropical waters of less than 30° C could have created mass annihilations by beaching a part of the indigeneous cephalopod fauna at localities 21, 22, 13, 14, 16, and/or 37 in the northern hemisphere season (Fig. 12, top) and 27, 31, and/or 32 in the southern hemisphere season (Fig. 12, bottom). From mid-latitude storm track maps we would suggest that localities 1, 5, and/or 6 in the northern hemisphere (Fig. 13, top) and 34, 35, 29, 30, 39, 40, and/or 41 in the southern hemisphere (Fig. 13, bottom) could contain chaotic assemblages of ammonoids and thus likely be faunal tempestite accumulations.

Should any of the ammonoid localities be deduced as a possible tempestite, the researcher will be able to identify the type of storm. Localities outside these predicted limits will further extend the potential boundaries of these storm types. The interaction between paleontologists and paleoclimate modelers will further advance this frontier in our science.

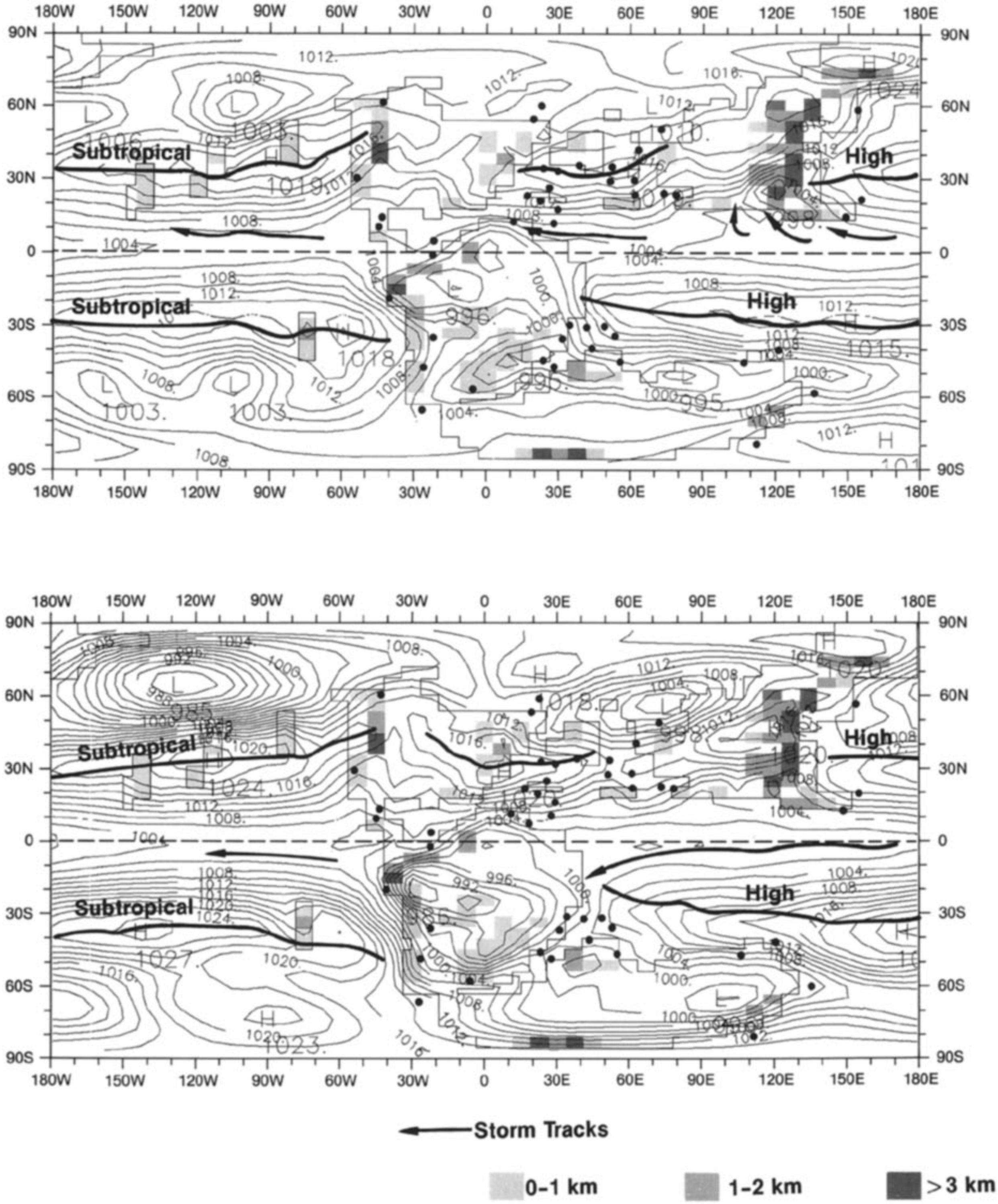

FIGURE 12—Aug/Sept/Oct (top) and Jan/Feb/March (bottom) sea level pressure (mb) map of Late Jurassic tropical cyclone seasons showing storm tracks with overprint of ammonoid localities. Paleotopography shown in model resolution format in 1 km intervals. See Moore et al. (1992a) for further discussion.

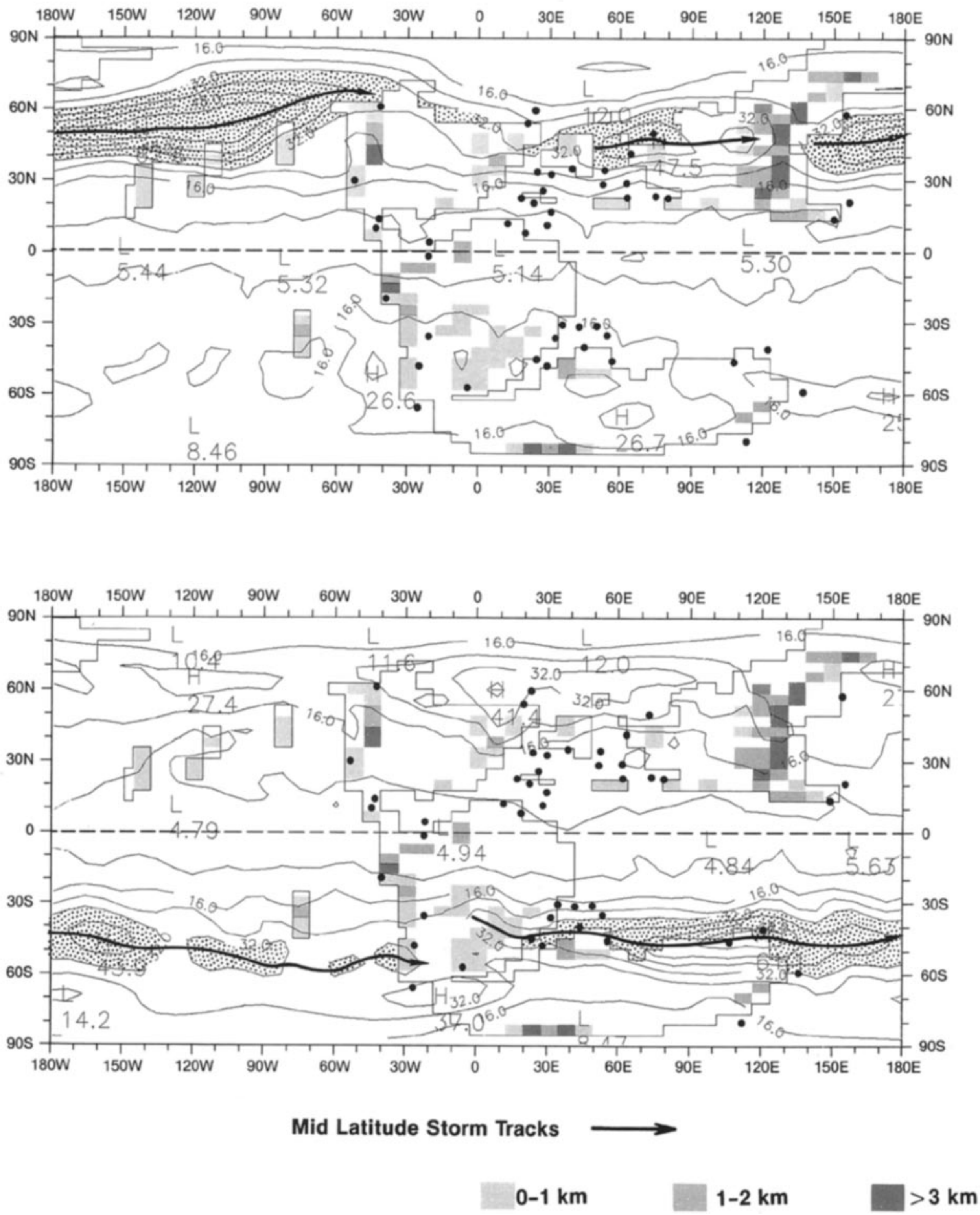

FIGURE 13—Dec/Jan/Feb (top) and June/July/Aug (bottom) Late Jurassic storm tracks from time filtered standard deviation of geopotential height field at 500 mb with overprint of ammonoid localities. Paleotopography shown in model resolution format in 1 km intervals. See Moore et al. (1992a) for further discussion.

CONCLUSIONS

By the Kimmeridgian and Tithonian stages of the Late Jurassic, two propagating rift systems out of the western Tethys Sea and a third persistent one between North America and Eur-Asia caused disintegration of the megacontinent Pangea. A rising sea level partially flooded the continents, particularly Eur-Asia. The extensive margins and epeiric seas hosted a wide-ranging cosmopolitan ammonoid fauna that became progressively provincial during the Tithonian.

Forty-seven Kimmeridgian and Tithonian ammonoid fossil localities worldwide can be grouped into two faunal realms made up of seven provinces. The two realms are joined in Europe by a narrow transition zone. The most distinctive is a Boreal Faunal Realm with a single province. Four other provinces occur in the Tethys and two in Panthalassa.

The SST range based on our CCM results indicates that, except for the Boreal Realm, ammonoid populations favored temperatures that were less than 30° C. Because ammonoid localities do not occur where modeled SST exceed 30° C, high SST may have been an environmental limit. On the other hand, some high latitude forms in the Boreal Realm lived in the SST range of 20° to 5° C and some faunas in high latitude northern hemisphere localities may have wintered under sea ice. The higher end of the temperature range for SST generally fits that of present-day *Nautilus*.

Results from analyses of P-E maps show that low-to-mid latitude ammonoid faunas generally favored seas with a negative P-E and with normal to higher-than-normal salinities. However, this paleoecologic parameter does not appear to dominate over others, such as temperature.

Wind-driven coastal upwelling correlates with high primary biologic productivity in today's ocean and that of the mid-Cretaceous. Comparison of Kimmeridgian and Tithonian wind-driven coastal upwelling in all seasons with ammonoid localities shows a strong positive correlation. Twenty-nine (63%) localities occur in grid cells with two or more seasons of upwelling whereas 39 (85%) occur in grid cells with one season. Seven (15%) grid cells contain localities with no upwelling.

Because the biology and geographic distribution of organisms relate to many physical, environmental, and historical factors, paleogeographic and paleoclimatologic data are invaluable in interpreting the dispersal patterns and phylogenetic relationships among different lineages within a taxonomic group. In this study, we conclude that the CCM is effective in assisting the biostratigrapher in interpreting the past habitat of ammonoids. Analysis of other groups of fossils may greatly benefit from this approach.

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