

Chapter 17

Biogeography of Kutch Ammonites During the Latest Jurassic (Tithonian) and a Global Paleobiogeographic Overview

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1 Introduction

The Late Tithonian ammonite-bearing horizons have very limited geographic occurrence in Kutch, being restricted only to the western part of the mainland. A 15 m thick sequence consisting mainly of oolite-shale alternations and coarse grained sandstone yields the terminal Tithonian faunal assemblages. The previous comprehensive report comes from Spath's work (1927–1933) where he described some Early Tithonian ammonites from farther east within the mainland, but the typical Upper Tithonian assemblages are restricted only to the westernmost part, i. e., towards the paleoshoreline (Fig. 17.1).

Spath described altogether seven genera of Late Tithonian age and these include mostly species of the genus *Virgatosphinctes* Uhlig. Stratigraphic knowledge of the Kutch ammonites was very poor during Spath's time and the collections were made mostly by other workers. Our repeated field investigations and systematic collections revealed that the Upper Tithonian assemblages are restricted mainly to the top part of the Umia Member (Mitra et al., 1979) (Fig. 17.2). The stratigraphic distribution of all species and genera described by Spath (1927–1933) has been firmly established on the basis of additional collection. In addition, our recent collection has unearthed many other genera of various

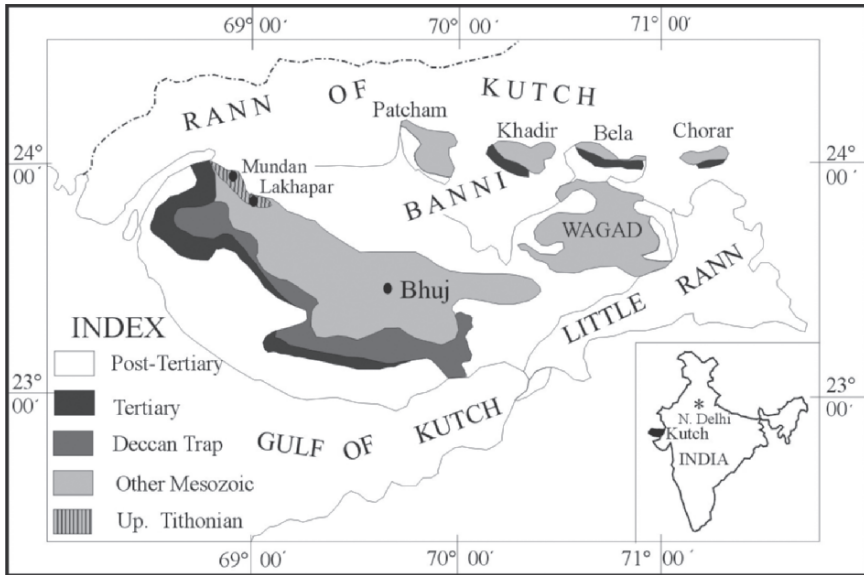


Fig. 17.1 Geological map of Kutch. Note small aerial extent of the Upper Tithonian beds.

provinces and different levels within the Upper Tithonian. These include *Durangites* Burckhardt, *Corongoceras* Spath, *Tithopeltoceras* Arkell, *Himalayites* Uhlig, and *Pterolytoceras* Spath (Shome et al., 2004; Shome et al., 2005; Shome and Roy, 2006). *Durangites* and *Micracanthoceras micracanthum* (Oppel) are the zonal indices of tropical Europe (see Cecca, 1999). It now appears that the Upper Tithonian assemblage in Kutch is represented by at least ammonites of three Mediterranean zones (cf. Tavera et al., 1986; Cecca, 1999).

The state-of-the-art of the Upper Tithonian ammonite assemblages of the world has been reevaluated in the light of new data and the nature of endemism and diversity patterns have been studied in the present endeavor. The Jurassic–Cretaceous boundary arguably marks a mass extinction event and ammonites evidently show a high extinction signal. We believe it is critical to understand the biogeography of the Late Tithonian ammonites in order to evaluate the patterns and extent of the end-Jurassic extinction event.

2 Upper Tithonian Assemblages of Different Faunal Provinces

The paleobiogeographic history of Mesozoic ammonites is marked by the repeated alternation of high degrees of provincialism and cosmopolitanism. The peak of ammonite provincialism occurred during the Late Jurassic and Early Cretaceous (Gordon, 1976). Different names were given for the Upper Jurassic stages in different regions because of this high endemism, i.e., Tithonian in the Tethyan and Indo-

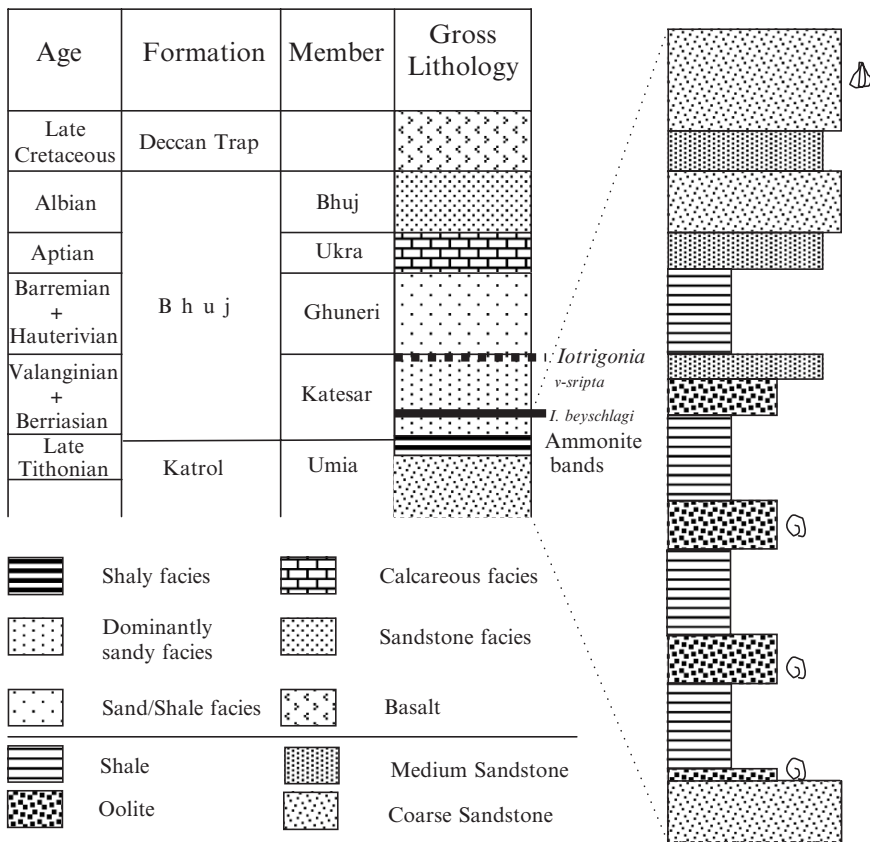


Fig. 17.2 Stratigraphic section showing the position of the Late Tithonian ammonites in Kutch (vertical thickness not to scale).

Pacific realms, Portlandian in southern England and Paris, and Volgian in Russia. Even within provinces, subprovinces can still be recognized, e.g., in the Mediterranean (see Cecca, 1999).

Because of the endemism of Tithonian ammonites, interprovincial correlation is a challenge and forms the focus of recent paleobiogeographic research (see references below). This has greatly improved our understanding of Tithonian ammonites, their paleobiogeography, oceanographic barriers, and migrational routes. Paleobiogeographic terminology is still in a state of flux and suffers from nomenclatural chaos because of the subjectivity involved (see for details Westermann, 2000a, b; Cecca and Westermann, 2003) and inherent complexity of the paleobiogeographical patterns (Dommergues, 2005, personal communication). We here try to follow the paleobiogeographic classification used by the leading workers (Riccardi, 1991; Enay and Cariou, 1997, 1999; Cecca, 1999, 2000; Zakharov and Rogov, 2003) of Tithonian ammonites and include the standardized terminology as

suggested by Westermann (2000a, b; 2005, personal communication) and Cecca and Westermann (2003) within parentheses. Following is a discussion of recent research results on the occurrences of Late Tithonian genera (“leiostracans” excluded) in different non-Boreal provinces/regions. A summary of results is presented in Table 17.1.

Table 17.1 List of Late Tithonian ammonite genera in different non-Boreal provinces/realms. x = present; * = genus survived the Jurassic–Cretaceous boundary.

	Indo-Madagascar	Mediterranean	Andean	Caribbean	Austral (Indo-Pacific)
<i>Anavirgatites</i>	x	—	—	—	—
<i>Andalusphinctes</i>	—	x	—	—	—
<i>Aspidoceras</i>	x	x	x	x	x
<i>Aulacosphinctes</i>	x	x	x	x	x
<i>Aulacosphinctoides</i>	x	—	—	—	x
<i>Baeticoceras</i>	—	x	—	—	—
<i>Berriasella</i> *	x	x	x	x	x
<i>Blanfordiceras</i>	x	—	x	—	x
<i>Bochianites</i> *	—	x	—	x	—
<i>Corongoceras</i>	x	x	x	x	x
<i>Curdubiceras</i>	—	x	—	—	—
<i>Dalmasiceras</i> *	—	x	—	—	—
<i>Danubisphinctes</i>	—	x	—	—	—
<i>Dickersonia</i>	—	—	x	x	—
<i>Djurjuriceras</i>	x	x	x	—	—
<i>Durangites</i>	x	x	—	x	—
<i>Haploceras</i> *	x	x	—	x	—
<i>Hemisimoceras</i>	x	x	—	—	—
<i>Hemispiticeras</i>	—	—	x	—	—
<i>Hildoglochiceras</i>	x	—	—	—	—
<i>Himalayites</i>	x	x	x	—	x
<i>Kossmatia</i>	—	x	—	x	x
<i>Lamencia</i>	—	x	—	—	—
<i>Lytogyroceras</i>	—	x	—	—	—
<i>Lytohoplites</i> *	x	—	x	x	x
<i>Malbosiceras</i> *	—	x	—	—	—
<i>Mazaplites</i>	—	—	—	x	—
<i>Micracanthoceras</i>	x	x	x	x	—
<i>Moravisphinctes</i>	—	x	—	—	—
<i>Nebroditis</i>	x	—	—	—	—
<i>Negrelliceras</i> *	—	x	x	x	—
<i>Neolissoceras</i> *	x	x	—	—	—
<i>Neoperisphinctes</i>	—	x	—	—	—
<i>Oloriziceras</i>	—	x	—	—	—
<i>Oxylenticeras</i>	—	x	—	—	—
<i>Paraulacosphinctes</i>	—	x	—	—	—
<i>Paraboliceras</i>	—	—	—	—	x
<i>Parapalliceras</i>	—	x	—	—	—

(continued)

Table 17.1 (continued)

<i>Parabilliceratoides</i>	—	—	—	—	x
<i>Parodontoceras</i>	—	—	x	x	—
<i>Pectinatites</i>	—	—	x	—	—
<i>Phanerostephanus</i>	x	—	—	—	—
<i>Proniceras</i>	x	x	—	—	x
<i>Protacanthodiscus</i>	x	x	x	—	—
<i>Protancyloceras</i>	x	—	—	—	—
<i>Pseudoargentinoceras</i>	—	x	—	—	—
<i>Pseudodiscosphinctes</i>	—	x	—	—	—
<i>Pseudoinvoluticeras</i>	x	—	x	—	—
<i>Pseudolissoceras</i>	—	—	x	x	x
<i>Salinites</i>	—	—	—	x	—
<i>Schaiveria</i>	—	x	—	—	—
<i>Simoceras</i>	—	—	x	—	—
<i>Simolytoceras</i>	—	x	—	—	—
<i>Simosphinctes</i>	—	x	—	—	—
<i>Simplisphinctes</i>	—	x	—	—	—
<i>Spiticeras*</i>	x	—	x	—	x
<i>Suarites</i>	—	—	—	x	—
<i>Subalpinites*</i>	—	x	—	—	—
<i>Subdichotomoceras</i>	x	x	—	—	x
<i>Substeueroceras</i>	—	x	x	x	x
<i>Substreblites*</i>	—	x	—	—	—
<i>Subthurmannia*</i>	—	x	—	—	—
<i>Tithopeltoceras</i>	x	x	—	—	—
<i>Umiaites</i>	x	—	—	—	—
<i>Vinalesites</i>	—	—	x	x	—
<i>Virgatosphinctes</i>	x	—	x	—	x
<i>Wichmanniceras</i>	—	—	x	—	—
<i>Windhauseniceras</i>	—	—	x	—	—
<i>Zittelia</i>	—	x	—	—	—

The Indo-Madagascan Province was well established since the Middle Jurassic (Arkell, 1956). During the Tithonian, the most fossiliferous regions are Kutch (Spath, 1927–1933), Baluchistan (Fatmi, 1972; Fatmi and Zeiss, 1994), and Madagascar (Collignon, 1960). The other areas included Somalia and Tanzania, from which only a few genera have been reported (see Enay and Cariou, 1997; Cecca, 1999). The Himalayan faunas, which show “sub-austral” affinity (Indo-Pacific of Westermann, 2000a, b) (see Enay and Cariou, 1997), are not included in this province. Previously it was believed (e.g., Cecca, 1999) that the Indo-Madagascan Late Tithonian ammonites were less diverse. The recent discoveries of several new ammonite genera from Kutch now reveal that this province is the second most diverse (see Table 17.1). Kutch, northwest Pakistan, and Madagascar together include 27 genera (Table 17.2) under four families: Olcostephanidae, Neocomitidae, Himalayitidae, and Aspidoceratidae.

Like other provinces, the Indo-Madagascan Province initially also shows well-marked endemism. The Early Tithonian is characterized mainly by many species of

Table 17.2 Late Tithonian ammonite genera present in three different regions of the Indo–Madagascan Province. Symbols are same as in Table 1.

	Kutch	Madagascar	NW Pakistan
<i>Anavirgatites</i>	–	x	–
<i>Aspidoceras</i>	–	–	x
<i>Aulacosphinctes</i>	x	x	x
<i>Aulacosphinctoid</i>	x	x	x
<i>Berriasella</i> *	–	x	–
<i>Blandfordiceras</i>	–	–	x
<i>Corongoceras</i>	x	x	–
<i>Djurdjuriceras</i>	–	x	–
<i>Durangites</i>	x	–	–
<i>Haploceras</i> *	x	–	x
<i>Hemisimoceras</i>	–	x	–
<i>Hildoglochiceras</i>	–	x	x
<i>Himalayites</i>	x	x	x
<i>Lytohoplites</i> *	–	x	–
<i>Micracanthoceras</i>	x	x	x
<i>Nebrodités</i>	x	–	–
<i>Neolissoceras</i> *	–	x	x
<i>Phanerostephanus</i>	–	x	–
<i>Proniceras</i>	–	x	x
<i>Protacanthodiscus</i>	–	–	x
<i>Protancyloceras</i> *	–	x	–
<i>Spiticerás</i> *	–	x	x
<i>Subdichotomoceras</i>	–	–	x
<i>Tithopeltoceras</i>	x	–	–
<i>Umiaites</i>	x	–	–
<i>Virgatosphinctes</i>	x	x	x

Virgatosphinctes (see Spath, 1927–1933). Endemism is so pronounced that even some leiostracans (e.g., *Pterolytoceras*) were exclusive to this province and Spiti Himalayas (Shome and Roy, 2006). Endemism became somewhat blurred, however, due to the invasion of many cosmopolitan forms during the Late Tithonian marine transgression (Haq et al., 1987; Hallam, 1992). The subfamily Virgatosphinctinae continued, but younger forms included a new stock having large body size (authors' personal observation).

In the Mediterranean Province, Late Tithonian ammonite assemblages are known only from a few areas in southern Spain, Italy, and France (see Cecca, 1999). Like Kutch, this province also experienced considerable reduction of the habitat due to regression, especially in the southern European platform and epicontinental basins (Fourcade et al., 1991; Cecca, 1999). However, southern Spain is highly fossiliferous and includes 33 genera (see Tavera, 1985). This is also the highest level of ammonite diversity in any region of the world during the Late Tithonian.

The Mediterranean assemblage was dominated by genera belonging to mainly three families. “Perisphinctidae” showed renewed diversity (Tavera, 1985) and

included 11 genera. The “Berriassellidae” were also equally diverse with 11 genera (Tavera, 1985). Additionally, Simoceratidae, which is typical of the Mediterranean facies during the Early Tithonian, persisted. Olcostephanidae and Opellidae were represented by sparse genera.

Leanza (1981) and Riccardi (1991) have analyzed the Upper Tithonian ammonite assemblages of the Andean Province. Three main fossiliferous areas are north-western South America, central-western South America, and southern South America. Their faunas are fairly homogeneous, but the similarity coefficient index varies from place to place (Riccardi, 1991). Each area includes Andean endemic genera which help in establishing intraprovincial correlation. Altogether, 25 genera have been recognized in this province. Assemblages in southern South America are slightly distinct in the sense that they show closer affinity with “Austral” New Zealand and “Ethiopian” (=Indo-Madagascan, described here) Madagascar. Even at the species level, this affinity is evident especially during the Late Tithonian (see below).

The Caribbean Province was first proposed by Westermann (1984) and Taylor et al. (1984) who used the term for the Middle Jurassic assemblages. On the basis of ammonite assemblages, Myczyński and Pszczolkowski (1994) suggested that this province was also well established during Late Jurassic and Early Cretaceous times. The province includes faunas of Cuba and Mexico.

The Tithonian ammonites of Cuba are moderately diverse. Myczyński and Pszczolkowski (1994) reported 13 genera from eight families. They are dominated by the cosmopolitan forms and some endemic taxa at the species level (see Cecca, 1999). The assemblages show mixed provincial characters dominated by Mediterranean faunas. However, geographically wide ranging genera like *Corongoceras*, *Himalayites*, *Durangites*, and *Aulacosphinctes* Uhlig, which are now described from Kutch (Shome et al., 2004), are also present. Myczyński (1989) mentioned many species of *Virgatosphinctes* including *V. denseplicatus*, which is a typical Indo-Madagascan form. However, Cecca (1999), and previously Enay (1972) and Callomon (in Hillebrandt et al., 1992), doubted the generic affiliation of this Cuban form.

In Mexico, ammonite assemblages show a fair degree of homogeneity (Imlay, 1939; Verma and Westermann, 1973; Olóriz et al., 1999) with the Cuban taxa. Verma and Westermann (1973) described altogether nine genera, including *Kossmatia* Uhlig, a genus not found in Cuba but typical of the “Austral Province” (Indo-Pacific Realm) (Enay and Cariou, 1997).

The Austral Realm (Indo-Pacific) covers east peri-Gondwanan areas including Antarctica (Thomson, 1980, 1982; Riccardi, 1991), New Zealand (Stevens, 1997), and Papua New Guinea (Indonesia) (Riccardi, 1991) and extends up to the Himalayas (see Enay and Cariou, 1997; Westermann, 2000b). This is a less diverse region as far as the Late Tithonian ammonites (14 genera) are concerned. Other than the Himalayas, Tithonian ammonites are poorly known from the rest of the areas. Recently, Enay and Cariou (1997, 1999) reported seven genera under three families, i.e., Olcostephanidae, Neocomitidae, and Himalayitidae from Spiti in India and the Nepal Himalayas. They mentioned that Himalayan forms are characterized by endemic taxa, which show some degree of Austral affinity. The family Neocomitidae

dominates the assemblage and includes three genera, *Berriasella* Uhlig, *Blanfordiceras* Cossmann, and *Corongoceras*.

Panboreal Superrealm ammonites are high latitude faunas living in the areas north of 45–50° N (Westermann, 2000a; Zakharov and Rogov, 2003). This belt was well established since the Middle Jurassic and correlation, therefore, between the Volgian and Tithonian is still a problem. However, during the Late Jurassic, Boreal–Tethyan ammonites show latitudinal shifts time and again, and thermally anomalous assemblages have been found in many Boreal areas indicating a northward migration of several Tethyan genera (see Zakharov and Rogov, 2003; and references therein).

The composition of Boreal ammonite assemblages during the latest Jurassic differs greatly from the contemporary Kutch faunas, which are essentially Tethyan in affinity. We follow Zakharov and Rogov (2003) in dividing the Panboreal Superrealm into four realms, Boreal West Europe (Northwestern Europe), Boreal East Europe (Volga Basin and Russian Platform), Boreal Pacific (Chukotka–Canadian Province and Primorje), and Boreal Eastern Pacific (British Columbia and California). We present the boreal data in a later section, to show diversity and extinction intensity. The genera characteristic of these regions are listed in Table 17.3 (Arkell, 1956; Arkell et al., 1957; Wright et al., 1996; Cecca, 1999; and Zakharov and Rogov, 2003; and references therein).

3 Affinity of Kutch Assemblage

It is already mentioned that the Upper Tithonian assemblages of Kutch can be correlated with the three biozones of the Late Tithonian of the Mediterranean Province. The lower assemblage in Kutch, however, is quite distinct and includes mostly virgatosphinctinid genera, especially the *Virgatosphinctes denseplicatus* group of species (Spath, 1927–1933; Krishna et al., 1996). *Virgatosphinctes denseplicatus* is typically restricted to peri-Gondwanan regions. In the upper part, *Virgatosphinctes* spp. continues, but they show evolutionary changes, becoming large and coarsely and distantly ornate. This kind of evolution has also been noticed in Spiti and Nepal (see Enay and Cariou, 1997), Baluchistan (Fatmi, 1972), and also in Madagascar (Collignon, 1960).

The Kutch assemblage also contains other faunas which show complex paleobiogeographic affinities. At the generic level, it shows affinity to various provinces. For example, *Tithopeltoceras*, which is only found in a restricted belt (30° N) within the Mediterranean Province has recently been described from Kutch (Shome et al., 2005). In addition, *Durangites*, which is found dominantly in the Mediterranean Province (Tavera, 1985; Cecca, 1999) and Mexico (Imlay, 1939; Verma and Westermann, 1973), has also been recorded from Kutch (Shome et al., 2004), while the austral *Himalayites*, is now found to have extended up to the Kutch basin (authors' personal observation). *Corongoceras* and *Micracanthoceras*

Table 17.3 Late Tithonian ammonite genera present in different Boreal realms. Symbols are same as in Table 1.

	Boreal West Europe	Boreal East Europe	Boreal Pacific	Boreal Eastern Pacific
<i>Aulacosphinctes</i>	—	x	x	—
<i>Berriasella</i> *	x	x	x	x
<i>Bochianites</i> *	x	x	—	x
<i>Chetaites</i>	—	—	x	—
<i>Craspedites</i>	—	x	—	—
<i>Cyrtosiceras</i> *	—	x	—	—
<i>Dalmasiceras</i> *	—	x	x	x
<i>Danubisphinctes</i>	x	—	—	—
<i>Dorsoplanites</i>	—	x	x	—
<i>Durangites</i>	—	x	—	—
<i>Glochiceras</i>	—	x	—	—
<i>Graniericeras</i> *	—	x	—	—
<i>Haploceras</i> *	x	x	—	—
<i>Kachpurites</i>	—	x	—	—
<i>Kossmatia</i>	—	—	—	x
<i>Lamencia</i>	—	x	—	—
<i>Lomonossovella</i>	—	x	—	—
<i>Negrelliceras</i> *	—	—	—	x
<i>Notostephanus</i>	—	—	—	x
<i>Praechetaites</i>	—	x	—	—
<i>Proniceras</i>	—	—	x	x
<i>Protancyloceras</i> *	—	x	—	—
<i>Pseudovirgatites</i>	x	—	—	—
<i>Spiticeras</i> *	x	x	—	x
<i>Subcraspedites</i> *	—	—	x	—
<i>Substeueroceras</i>	—	—	—	x
<i>Substreblites</i> *	—	—	—	x
<i>Sutneria</i>	—	x	—	—
<i>Titanites</i>	—	—	—	x
<i>Zaraiskites</i>	x	—	—	—

Spath are cosmopolitan genera and they also have been found in Kutch (Spath, 1927–1933; Shome et al., 2004). *Pterolytoceras*, a leiostracan, has recently been recovered from Kutch (Shome and Roy, 2006). This genus was earlier reported from Tithonian beds of Madagascar, northwestern Pakistan, and Spiti Himalayas (Collignon, 1960; Fatmi, 1972; Krishna et al., 1982). It is found in shallow water sediments with other genera in Kutch. The restricted paleobiogeographic distribution of *Pterolytoceras* also suggests its shallow water habitat (see Shome and Roy, 2006). It is endemic, short lived, and restricted only to the Indo-Madagascan Province.

The high faunal diversity of Kutch is compatible with the sea level rise during the Late Tithonian (see Haq et al., 1987; Hallam, 1992), which facilitated some

degree of faunal exchange and long-distance migration of faunas among different provinces (see also Shome et al., 2005). The ammonite-bearing Late Tithonian rocks are green, glauconitic oolites that intercalate with shales. They are the product of the Maximum Flooding Zone (MFZ) (Fürsich and Pandey, 2003).

We have made an attempt to establish faunal correlation at the genus level among different non-Boreal provinces and regions using the Jaccard coefficient (see Table 17.4). The low Jaccardian coefficient (cf. Campbell and Valentine, 1977) suggests the persistence of endemism among the regions during the Late Tithonian. Even within the Indo-Madagascan Province, the correlation coefficient values are low (Table 17.5). This is because each major region has its own endemic genera and relative endemism varies from place to place (18%, 35%, and 29% respectively for Kutch, Madagascar, and northwest Pakistan). Das (2003) recognized different correlation coefficients within the Indo-Madagascan Province based on Jurassic–Cretaceous gastropod data and he suggested Kutch be considered as a separate sub-province. The boreal faunal correlation coefficient also having low values is shown in Table 17.6.

Table 17.4 Jaccard similarity coefficients of Late Tithonian ammonite genera between area pairs in different non-Boreal provinces/realms.

	Indo-Madagascan	Mediterranean	Andean	Caribbean	Austral (Indo-Pacific)
Indo-Madagascar	–	0.23	0.34	0.22	0.25
Mediterranean	0.23	–	0.17	0.26	0.17
Andean	0.34	0.17	–	0.43	0.31
Caribbean	0.22	0.26	0.43	–	0.28
Austral	0.25	0.17	0.31	0.28	–

Table 17.5 Jaccard similarity coefficients of the Late Tithonian ammonite genera between area pairs in different basins of the Indo-Madagascan Province.

	Kutch	Madagascar	NW Pakistan
Kutch	–	0.27	0.25
Madagascar	0.27	–	0.41
NW Pakistan	0.25	0.41	–

Table 17.6 Jaccard similarity coefficients of the Late Tithonian ammonite genera between area pairs in different provinces of the Boreal Realm.

	West Europe	East Europe	Pacific	Eastern Pacific
West Europe	–	0.19	0.08	0.20
East Europe	0.19	–	0.19	0.16
Pacific	0.08	0.19	–	0.20
Eastern Pacific	0.20	0.16	0.20	–

4 Migrational Routes and Paleolatitudinal Disposition of Kutch

The above mentioned Late Tithonian assemblage of Kutch thus suggests a complex pattern of migrational history of ammonite taxa from different provinces and at the same time dispersal of endemic forms (species level) to other areas. The presence of genera previously known in different provinces indicates a grand migrational event during the global sea level rise. This large scale transgression helped establish seaway connections among various isolated or semi-isolated basins. Many of the immigrant genera in Kutch are cosmopolitan or have wide geographic ranges and their distribution at genus level are of little use in tracing migrational routes. Biogeographical and ecological patterns operate at species level (see Campbell and Valentine, 1977: 47). *Corongoceras* and *Micracanthoceras* are cosmopolitan genera but their species distributions show different paleobiogeographic patterns. For example, *Corongoceras lotenoense* was previously recorded from the Andes, Madagascar, Subbetic Mediterranean, and the Nepal Himalayas (Collignon, 1960; Matsumoto and Sakai, 1983; Riccardi, 1991). It has now been obtained from the uppermost Tithonian horizons in Kutch (Shome et al., 2004). A very narrow strait is thought to have opened up between South Africa and India during Late Jurassic time, which facilitated the excursion of faunas from Kutch to the Andes and vice versa. *Corongoceras lotenoense* from the Andes invaded Madagascar, Kutch, and the Himalayas (Riccardi, 1991), while younger forms of *Virgatosphinctes* spp. with large size migrated to Andean regions. Bivalve distributions also support the appearance of a South African corridor. *Megacucculea* (Lamarck), for example, which is thought to be endemic to the Indo-Madagascan area (Cox, 1940; Shome et al., 2004), sneaked into the Andean Province through this narrow corridor (see also Riccardi, 1991). *Eselaevitrigonia* (Kobayashi and Mori) which originated in Kutch during the same time, could not however, cross the seaway and consequently spread to the austral region only during a subsequent transgression in the Aptian (authors' personal observation).

Many ammonite species that migrated to Kutch from the Mediterranean or Himalayan regions could not cross the narrow strait presumably because of a temperature gradient or shallowness of the passage. They are *Micracanthoceras micracanthum* and species of *Durangites*, *Tithopeltoceras*, and *Himalayites*. *Micracanthoceras* has a wide paleobiogeographic distribution, but its type species, *M. micracanthum*, shows a different pattern. This species is used as a zonal index in the Mediterranean Tethys (Enay and Geysant, 1975), demarcating the Upper Tithonian boundary. It is also known from Mexico (Imlay, 1939) and Kutch (Spath, 1927–1933), but is conspicuously absent in the Austral and Andean provinces. This indicates that it likely came to Kutch from the northern Tethyan region. That the sea strait was narrow and shallow can also be understood by the relative diversity of leiostracans (including endemic *Pterolytoceras*; see Shome and Roy, 2006) restricted to Kutch and Madagascar (Spath, 1927–1933; Collignon, 1960). Many of these taxa, being oceanic and deep-water forms (see Westermann, 1990) could not get past this corridor.

Himalayatidae also participated in this “bioevent par excellence.” *Blanfordiceras* and *Spiticeras*, the two typical genera of the Himalayas, are also found in Baluchistan, Madagascar, and in the Andean Province. But they are still absent in Kutch, which we believe is perhaps due to collection failure. *Himalayites*, another typical Himalayan form is now known to extend up to Kutch.

Spath (1927–1933) described a new endemic genus *Umiates* Spath from Kutch and reported two species, *U. rajnathi* Spath and *U. minor* Spath. We have recently collected additional specimens and studied Spath’s type material kept in the repository of the Geological Survey of India in Kolkata. His two species appear to be conspecific and *Umiates* specimens are large, septate, and macroconchs. Detailed taxonomic analysis (to be published elsewhere) reveals that *Umiates* is very close to microconchiate *Proniceras* Burckhardt and they may form a dimorphic pair. During the Late Tithonian, *Proniceras* had a paleobiogeographic distribution in the Subbetic Mediterranean (Tavera, 1985), Mexico (Imlay, 1939), Baluchistan (Fatmi, 1972; Fatmi and Zeiss, 1994), Nepal Himalayas (Enay and Cariou, 1997), and Madagascar (Collignon, 1960). Thus, like many other forms, it also showed southward migration during the Late Tithonian.

Tithopeltoceras was reported only from the Mediterranean Province until recently (Shome et al., 2005). It is a “strange” genus (Enay, 1973; Olóriz and Tavera, 1979; Tavera, 1985), even within this province. It has restricted occurrences in the Micracanthum Zone of southern Spain, central Italy, and the Balearic islands and thus is distributed in a very narrow zone coinciding with the 30°N paleolatitude. This narrow latitudinal distribution was perhaps constrained by temperature. *Tithopeltoceras* has now been found in Kutch and significantly, the paleoposition of Kutch during the Tithonian was also 30°, but south of the equator (Shome et al., 2005). Other genera of Himalayatinae had a wide biogeographic spread (Olóriz and Tavera, 1989; Cecca, 1999). *Tithopeltoceras* perhaps being stenothermal was restricted mainly in the subtropic zone, on either side of the equator.

5 Paleobiogeography of Mass Extinction

Study of the diversity, distribution patterns, and endemism of the Late Tithonian ammonites is especially important because soon, at the end-Tithonian, the majority of them died. Arguably, the end of the Jurassic marks a mass extinction event (Raup and Sepkoski, 1986; but for an opposite view, see Hallam, 1986; and Hallam and Wignall, 1997). Hallam (1986) claimed that family level extinction data of ammonites are not impressive, but he admitted that taxonomic resolution down to lower level along with stratigraphic precision can only help in understanding the extent of extinction. Since then, floods of information on ammonite diversity, paleobiogeography, and refinements of stratigraphic ranges across the Jurassic–Cretaceous boundary have emerged (e.g., see Fatmi and Zeiss, 1994; Tavera et al., 1986; Riccardi, 1991; Enay and Cariou, 1997; Cecca, 1999; Olóriz et al., 1999;

Zakharov and Rogov, 2003; and many others) and a new treatise on Cretaceous ammonites has appeared (Wright et al., 1996). Literature scanning reveals that out of 84 ammonite genera (excluding leiostracans) of the Late Tithonian, 67 did not pass the Jurassic–Cretaceous boundary, thus showing a significant extinction signal (80%). Hallam (1986) tried to show that the end-Jurassic extinction event is of moderate scale and regional in nature. But many other workers also have investigated the extinctions of other organisms during the end-Tithonian and found significant extinction peaks. For example, Kelly (1984–92) analyzed bivalve data of England and Zakharov and Yanine (1975) also demonstrated extinction on the basis of Central Russian bivalves. In both areas, bivalve diversity was reduced significantly. Ager (1975, in Hallam, 1986), Davis (1975, in Hallam, 1986) and Sandy (1988) attempted to assess brachiopod mortality across the Jurassic–Cretaceous boundary, while others studied foraminifers (e.g., Jenkins and Murray, 1981), coccoliths (Hamilton, 1982) and ostracods (Ascoli et al., 1984; Whatley, 1988). All of them noted a major turn over of taxa at the boundary. More significantly, like the K–T boundary extinction, the Jurassic–Cretaceous extinction event also affected terrestrial and taxonomically different biota. Bakker (1993) recognized near-total extinction of plesiosaur reptiles and Benton (1995) claimed greater mortality of continental faunas at family level than of marine groups at the end of the Tithonian. It would be interesting to know, therefore, the biogeographic distribution patterns of the Late Tithonian ammonites which may, in turn, help in understanding the nature and causes of the extinction (also see Raup and Jablonski, 1993).

Late Tithonian ammonite genera have wide geographic distribution. Longitudinally, they are found from the boreal eastern Pacific to Austral Indonesia and the latitudinal distribution ranges from the Arctic regions in the north to Antarctica in the southern hemisphere. There are at least 60 major fossil occurrences in the world from where different assemblages of Late Tithonian ammonites have been recorded (see Cecca, 1999; Zakharov and Rogov, 2003). Since the number of genera in many localities is few and the Late Jurassic ammonites overall show strong endemism, we have plotted diversity data on a provincial, subprovincial, and regional basis (Fig. 17.3). Geographic and stratigraphic distributions have been drawn from the literature cited above and are also subjected to an updating and evaluation procedure. Stratigraphic ranges of some genera have been shown to be different in different literature, but we follow the data provided by the new Treatise (Wright et al., 1996).

The distribution of ammonite genera shows a broad latitudinal gradient with diversity decreasing towards at least the South Polar Region (see also Tables 17.1–3). Diversity is maximum in the subtropics on either side of the equator. The Mediterranean diversity is represented by 44 genera and in the south, the Indo-Madagascan Province and the Himalayas include 29 genera (see Fig. 17.3 and Tables 17.1–2). Similar trends of different taxa also existed during other mass extinction events such as the K–T (see Stanley, 1984, 1988; Jablonski, 1986; Zinsmeister et al., 1989). High latitude Tithonian ammonites were more diverse in some provinces in the northern hemisphere than in the southern hemisphere. This is due to latitudinal shifts towards the north shown by many Tethyan genera during the Late Tithonian (see Zakharov

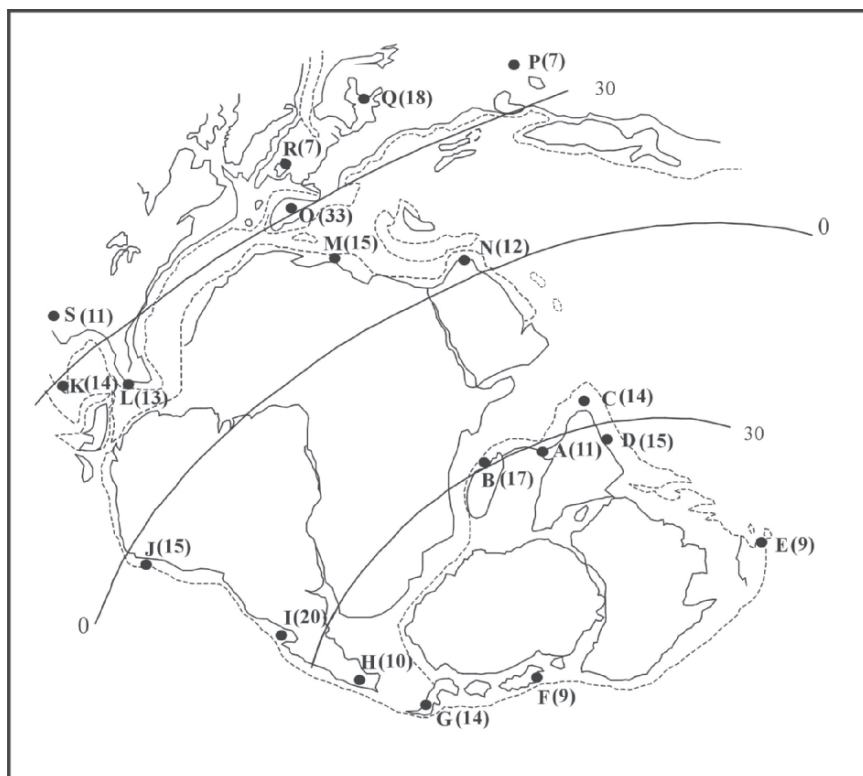


Fig. 17.3 Diversity of ammonite genera in different regions during the Late Tithonian. The base map is modified after Enay and Cariou (1997). A = Kutch; B = Madagascar; C = Northwest Pakistan; D = Himalayas; E = Indonesia; F = New Zealand; G = Antarctica; H = Southern South America; I = Central-West South America; J = Northwestern South America; K = Mexico; L = Cuba; M = North Africa; N = Iraq; O = Southern Spain; P = Boreal Pacific, shown at Primorje; Q = Boreal East Europe, shown at Crimea; R = Boreal West Europe, shown at England; S = Boreal Eastern Pacific, California. Sources are mentioned in the text.

and Rogov, 2003; and references therein). Climatic equability during the entire Jurassic was envisaged by Hallam (1969). Since the Arctic taxa are not found south of 30° N, Zakharov and Rogov (2003) believed in the existence of a temperature gradient during the Late Jurassic – Early Cretaceous period. Jeletzky (1984) also suggested a cooling event during the terminal Tithonian on the eastern coast of the Paleopacific. In addition to fossil data, recent general circulation model simulations of the Jurassic climate also reveal latitudinal thermal gradients at certain times and a semi-arid climate in many tropical areas especially during the Late Jurassic – Early Cretaceous (Page, 2005). Our study on *Tithopeltoceras* also shows latitudinal control on ammonite distribution (Shome et al., 2005). Surprisingly, high latitude southern hemisphere Austral faunas are marked by low endemism (12%).

The Majority of Late Tithonian ammonite genera became extinct at the Jurassic–Cretaceous boundary (80% as mentioned earlier). We intend here to study the extinction intensity of ammonites in different areas and to know whether there is any geographic control on extinction intensity. During the K–T extinction, some workers believe (e.g., Copper, 1977; Stanley, 1988; Banerjee and Boyajion, 1996; but see Raup and Jablonski, 1993, for a different view), that tropical areas were more severely affected than temperate or polar regions. This is envisaged because tropical taxa show greater endemism than cold water forms (Jablonski, 1986). We have followed Raup and Jablonski (1993) in choosing the extinction metric for our analysis. According to them “extinction was quantified as the proportion of genera found in an assemblage, or local group of assemblages, that suffered global extinction in the final stage” This is adopted here mainly because of the rarity of truly continuous stratigraphic sections across the Jurassic–Cretaceous boundary, and direct comparison of assemblages immediately below and above the boundary would result in only a limited analysis. However, unlike Raup and Jablonski (1993), we have included only Late Tithonian genera and thus have avoided genera which became extinct during the Early Tithonian (cf. Hallam, 1986). Otherwise, extinction

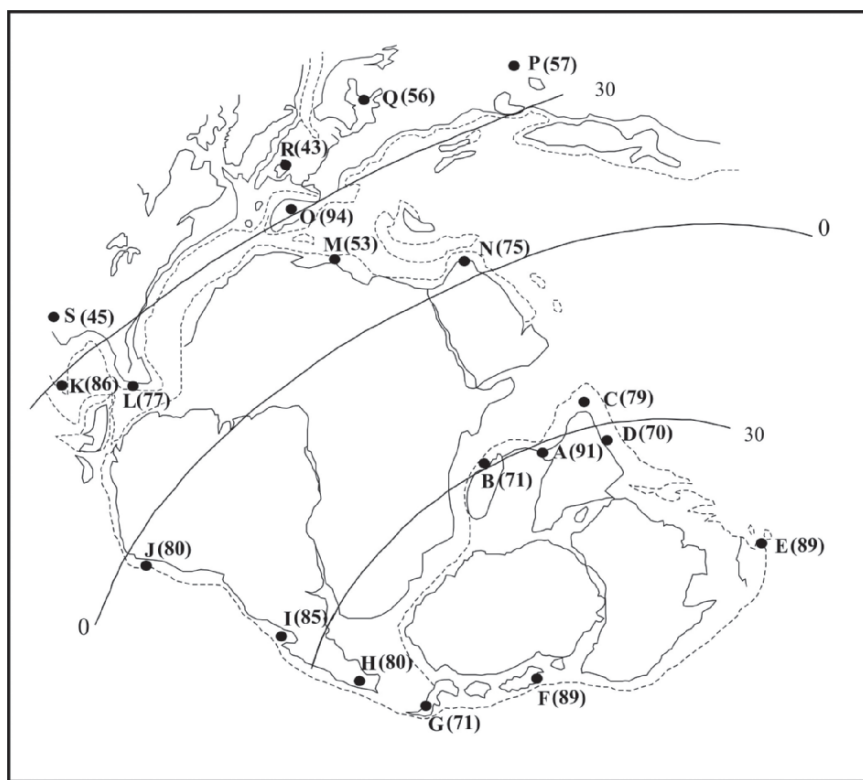


Fig. 17.4 Extinction intensity (percentage) in important fossil-bearing occurrences shown in Fig. 17.3.

values at the Jurassic–Cretaceous boundary would be artificially elevated. Extinction percentages of different provinces/regions are plotted in Fig. 17.4.

Extinction appears to be high and uniform throughout the world except in the Panboreal Superrealm. Here, the mean extinction is 50%. This is mainly for two reasons. First, some Boreal realms have low diversity (see Fig. 17.3). Second, the Panboreal Superrealm was invaded by many Tethyan genera during the Late Tithonian (see Table 17.3), some of which survived the Jurassic–Cretaceous boundary crisis (for details see below). In the boreal west Pacific Realm, diversity is less; of seven genera, three are Tethyan forms which crossed the Jurassic–Cretaceous boundary, but surviving genera are inevitably pooled in the global data, thus decreasing the regional extinction percentage. The majority of Boreal endemics (12 out of 15, i.e., 80%) as well as all immigrant genera died out in these areas during the J–K transition. If the Tethyan genera are removed from the count, the “sanctuaries” of extinction in northern higher latitudes disappear and the mean extinction becomes 86%. Thus, extinction patterns show no gradient across either latitude or longitude. The mean extinction is 73% and the median is 77%. This indicates a quite high extinction signal all over the world.

Kutch and the tropical Mediterranean southern Spain have higher extinction percentages (91% and 94%, respectively) and can be considered as “hot spots” of extinction. In Kutch, although the lowermost Cretaceous includes marine strata, the basin became extremely shallow (Biswas, 1977). Few gastropod and bivalve genera survived the Jurassic–Cretaceous boundary, but they also show species level turnover (Das, 2002; authors’ personal observation). All ammonite genera including leiostracans suffered regional extermination (Bardhan et al., 1989). Admittedly, the present extinction metric has the disadvantage that it fails to locate a local hot spot because the genera that died in that area may have survived elsewhere. In Kutch it so happened that all the genera also went extinct globally, so that this local hot spot was not hidden by this effect. This is perhaps due to the fact that the Kutch Sea harbored shallow water faunas which suffered most during the extinction.

The Mediterranean Province has an unusual number of endemics. A total of 14 of the 33 genera in Spain are endemic (42%) and none of them crossed the J–K boundary. This has greatly increased the extinction value. Kutch and southern Spain were located in the subtropical latitudes, but we do not believe that these areas were worst hit during the extinction. The high latitude Austral faunas (in spite of low endemism) have higher extinction values than other tropical areas.

Analysis of 17 genera surviving the extinction indicates that they belong to six families out of nine which persisted up to the Late Tithonian. Neocomitidae were most diverse (14 genera at the J–K boundary of which seven genera entered into the Cretaceous). Unfortunately, we do not have at present the species level database of all genera and, therefore, cannot tell whether any selectivity of survival of species-rich genera existed. However, three successful genera, i.e., *Berriasella*, *Lytrochoplites*, and *Spiticeras* were diverse during the Late Tithonian (see Collignon, 1960; Tavera, 1985).

The surviving tropical genera quickly diversified immediately after the boundary in the earliest Berriasian and belonged to two important families (Neocomitidae and Olcostephanidae) of the Early Cretaceous (see Wright et al., 1996, Table 17.2). It is tempting to suggest that like background extinction, cosmopolitan genera are resistant

to mass extinction (see Jablonski, 1989) at the Jurassic–Cretaceous boundary. However, 13 of the 19 cosmopolitan genera (with at least distribution in more than two provinces, see Table 17.1) went extinct. One selective element, however, becomes apparent; of 15 Tethyan genera which show climatic shifts towards northern high latitudes (see Table 17.3), eight survived the J–K boundary crisis. This perhaps suggests their ability to maintain range expansion in times of environmental stress. We have excluded leiostracan data from our analysis. Leiostracans have a higher rate of survival (only 30% became extinct) and were present in the Early Cretaceous both in the tropical and extratropical areas (Arkell et al., 1957; Wright et al., 1996; and Shome and Roy, 2006). Leiostracans, which are believed to be offshore dwellers (not necessarily deeper water, see Kennedy and Cobban, 1976; Bardhan et al., 1993), have lower extinction rates throughout the Jurassic (House and Senior, 1981).

The Late Tithonian ammonites are in general less diverse or poorly known from the whole Mediterranean Tethys (Cecca, 1999). This is due to large-scale destruction of the southern European platform and epicontinental habitat attributed to marine regression (Fourcade et al., 1991). But in southern Spain the situation was quite different. Here the ammonites were the most diverse in the world (33 genera, see Table 1, and Tavera et al., 1986) and belong to the Ammonitico Rosso facies, which represented the pelagic, epiocceanic environments including submarine highs (see Cecca, 1992; Cecca, 1999). This area is one of the rare sites where continuous sections across the Jurassic–Cretaceous boundary and the earliest Cretaceous ammonite assemblages are found (Tavera, 1985; Cecca, 1998). *Berriasella*, which suffered regional extinction elsewhere, crossed the boundary here and diversified quickly afterwards (see Tavera, 1985; Tvera et al., 1986). There is a general agreement that the Jurassic–Cretaceous boundary interval witnessed a major sea level lowering and regression took place in all provinces (e.g., Cecca, 1999; Zakharov and Rogov, 2003). This may be one of the causal factors of large-scale extinction of the Jurassic ammonites and other groups. A few genera survived, perhaps due to chance, with areas like Subbetic Spain serving as an “island refugia” (see Kauffman and Erwin, 1995) where *Berriasella* and several other Mediterranean genera survived.

In conclusion, analysis of the biogeography of the end-Jurassic ammonites reveals that extinction is homogeneous throughout the world. It shows no selectivity by latitude (except a few extinction “hot spots”) and geographic range (both endemic and pandemic groups suffered equally). Shallow water forms suffered most, while pelagic leiostracans have significantly lower extinction intensity, but this is due to low extinction rate in this group during the entire Jurassic. The Jurassic–Cretaceous ammonite extinction pattern is consistent with that observed in bivalves during the K–T mass extinction event (see Raup and Jablonski, 1993; Jablonski and Raup, 1995).

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