Control of climate and Tethyan legacy on distribution of Paleocene–Eocene gastropods and establishment of the Northern Tropical Realm

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Palaeobiogeographical distribution of gastropod genera from the Paleocene and the Eocene has been analysed. Based on this distribution, formal palaeobiogeographical provinces have been established and their relationships are sought. It has been found that the provinces were largely restricted to the palaeo-tropics and subtropics mainly of the northern hemisphere and they share a large proportion of their generic composition. The Northern Tropical Realm has been established to include these provinces. The distribution evinces presence of ocean surface currents in the tropics across longitudes. The possible currents moved through the relict Tethys Ocean, across the Atlantic Ocean and perhaps also across the Pacific. However, planktotrophic larvae of these benthic molluscs could not cross the deep ocean barrier that lay between the Northern Tropical Realm and the Austro-New Zealand Province of the southern hemisphere. The gastropod fauna in the latter province evolved independently. Distribution of all the provinces within palaeo-tropics and subtropics indicates strong control of temperature over it. Paleocene–Eocene Thermal Maximum appears to be responsible for extinction and range contraction of high latitude faunas. Low latitude faunas also suffered significant extinction. However, large diversification in the Eocene was a response to widespread transgression that coincided with the thermal event.

Keywords. Palaeobiogeography; Gastropoda; Paleocene; Eocene; Northern Tropical Realm; Paleocene–Eocene Thermal Maximum.

1. Introduction

The big biotic crisis at the end of Cretaceous left the world in jitters. The Upper Cretaceous and the early Paleogene are the times when the Earth was going through dramatic rearrangements due to huge tectonism. The Gondwana broke apart and the Indian plate started its great voyage in the Upper Cretaceous. The voyage continued

well within the Paleogene. The plate crossed the equator and reached the northern hemisphere, thereafter collided with the Tibetan plate causing disappearance of the Tethys Ocean leaving only a remnant, largely land-locked seaway of the modern Mediterranean. The formation of the Atlantic Ocean took place in different phases that also continued to the Cenozoic. These tectonic movements drew the present-day picture of the earth's surface.

This large scale re-distribution of land and sea should have brought significant changes in the distribution of marine and terrestrial organisms, and thus, the shape and relationship of biogeographical units. It is interesting to see how the emaciated biosphere of the early Paleogene behaved in this time of turmoil when large scale tectonic movement and rearrangement of plates were taking place.

The early Paleogene is also interesting because the Paleocene–Eocene boundary witnessed a very sharp increase in global temperature along with emission of large quantity of CO₂ in the atmosphere. This phenomenon, known as the Paleocene–Eocene Thermal Maximum (PETM), was followed by other spikes in the temperature curve during the early Eocene. This phase of global warming has been documented to have caused significant changes in the biotic composition of higher latitudes. It is generally believed that tropical biota was not significantly affected because with rising temperature climate generally becomes globally more equable and the tropical climatic zone latitudinally widens. Higher latitudes, on the contrary, lose their biota with warming because favourable climate for organisms thriving there is not to be found anywhere in the world. However, a sharp rise in temperature like that in the PETM can have an unusual effect because of its rapidity. It may be pertinent to mention that the tropical biota of the Eocene was not adequately documented from this point of view (Samanta *et al.* 2013).

Benthic molluscs have remained a formidable group in the marine ecosystem throughout the Phanerozoic in terms of diversity, abundance, and morphological and ethological disparity. Their dispersal mechanism, involving planktotrophic larval ontogeny and depending on oceanic currents, can fruitfully be used in deciphering migration routes and reconstruction of ancient ocean currents. During the Cenozoic in the marine benthic habitat molluscs are the most diverse group. Analysis of their distribution often reveals interesting results (e.g., Piccoli *et al.* 1991; Popov 1993; Harzhauser *et al.* 2002). Such analyses involving benthic molluscs during the time interval of Paleocene–Eocene, which has gone through major tectonic re-arrangements and climatic perturbations should throw light on many unlit corners of their life-history.

Here, we study distribution pattern of the Paleocene–Eocene gastropod genera for palaeobiogeographical analyses. We have gathered distribution data of all the Paleocene and the Eocene

gastropod genera, and plotted them in palaeo-coastline maps (Smith *et al.* 1994) to (1) figure out the global distribution pattern of gastropods, (2) erect formal palaeobiogeographical units, and (3) seek possible relationships between the units. Quantitative analyses have also been done here to assess relative contributions of tectonism and global warming events in shaping the geographical and latitudinal distribution patterns and their changes through the Paleocene to the Eocene. This, we hope, will form the basic framework for further finer scale analyses.

2. Materials and methods

All the gastropods belonging to the Paleocene and the Eocene have been tabulated from Sepkoski's compendium (Sepkoski 2002). This is the most updated and comprehensive resource containing the hierarchical data of all the invertebrates. Table 1 gives a summary account of families and genera in the Paleocene and the Eocene along with extinction in the former and new appearance in the latter. The generic data have been taken into account for this study. The status of the generic data was checked with online molluscan database *Mollusca Base* (2016), palaeobiological database 'Fossilworks' (2016), and biological database WoRMS (2016). *Fossilworks* (2016) also provided the geographical distribution of the genera. The distribution data for the genera belonging to each of the gastropod families of the Paleocene and the Eocene were plotted on the palaeo-coastline maps of Smith *et al.* (1994). This has been done for all the families. A few families showing high generic diversity have been considered as representatives in this study and only their distribution in the maps are shown here for the sake of convenience (figures 1.1–1.4 and 2.1–2.4). We have used 60 (Paleocene) and 45 Ma (middle Eocene) maps (Smith *et al.* 1994) as representing the Paleocene (66–56 Ma) and the Eocene (56–33.9 Ma; see Cohen *et al.* 2013), respectively. The temporal data for genera are sometimes not very precise and given as Paleocene and Eocene (Sepkoski 2002). Even though this analysis has its limitations due to such less precise temporal data and consideration of the whole epoch in a single time frame, it was still able to give a picture of broad geographical distribution pattern and its change through the geological time in question. Palaeobiogeographical provinces have been defined based on an inspection of these distribution patterns on the maps (table 2; figures 1.5

Table 1. *Summary account of gastropod families and genera of the Paleocene and the Eocene.*

No. of families		120
No. of families present in Paleocene		96
Families became extinct in Paleocene	Number	4
	Percentage	4.17
No. of families common to Paleocene and Eocene		92
No. of families present in Eocene		116
Families appeared in Eocene	Number	24
	Percentage	20.69
No. of genera		701
No. of genera present in Paleocene		387
Genera became extinct in Paleocene	Number	62
	Percentage	16.02
No. of genera common to Paleocene and Eocene		325
No. of genera present in Eocene		639
Genera appeared in Eocene	Number	314
	Percentage	49.14

and 2.5). Genera restricted to each of the provinces have been counted and their percentages calculated for the Paleocene and the Eocene (tables 3 and 4, respectively). The generic endemism reflects identity of a province and used in its definition.

The generic distribution data were then used for preparation of interprovincial similarity matrices. Number of common genera was counted for each pair of provinces to get the absolute generic similarity between any two provinces. Percentages of similarity between any two provinces are calculated with respect to the total number of genera present in each of the provinces following the formulae

(1) (genera common between provinces A and B/total number of genera in province A) $\times$ 100, and

(2) (genera common between provinces A and B/total number of genera in province B) $\times$ 100.

That gave two percentage values for each pair of provinces. Similarity matrices for the Paleocene and the Eocene, which show the diversity, and the absolute number and percentages of interprovincial similarity between each of the provinces are given in tables 5 and 6, respectively.

We have done a detailed analysis of latitudinal distribution of the genera for the Paleocene and the Eocene. For this, 10° latitudinal distances are considered (e.g., 0–10°N, 10–20°N, etc.) and genera present in each such bin are counted for both the epochs. Column diagrams were drawn from these data, which show latitudinal distribution of generic diversity and its change through the Paleocene to the Eocene (figure 3). 30–50°

latitudes in both the hemispheres appear to house maximum generic concentration in the epochs concerned (figure 3). The genera that went extinct in the Paleocene and those that appeared in the Eocene were counted in three latitudinal divisions, which are <30°, between 30 and 50° and >50° for both the hemispheres (table 7; figure 4). Genera present in more than one divisions are counted separately for all such divisions. Latitudinal range and its modification from the Paleocene to the Eocene of each of the genera that are common to both the epochs have been studied in the same three divisions, i.e., <30°, 30–50° and >50°, for both the hemispheres. An account has been prepared by counting the number of genera that in the Eocene, show (1) extension towards higher latitudes, (2) extension towards lower latitudes, (3) no change in range and (4) range contraction (table 8).

3. Results

701 genera belonging to 120 families have been recorded in the Compendium (Sepkoski 2002). 639 genera were present in the Eocene, whereas only 387 were there in the Paleocene. 62 genera of the Paleocene did not continue in the Eocene, while 314 new genera appeared in the latter epoch. So about 16% of the Paleocene genera became extinct whereas the Eocene witnessed appearance of about half of its genera and over 20% of its families (table 1). However, majority of the families have

The features of the distribution that immediately attract attention once one sees the maps (figures 1 and 2) frequency distribution across

latitudes (figure 3), values of endemism (tables 3 and 4) and similarity matrices (tables 5 and 6) are: (1) the distribution of gastropods appears to be largely restricted within palaeo-tropical and subtropical latitudes during the Paleocene and the Eocene, (2) diversity of gastropods is much higher in the Northern Hemisphere than that found in the Southern Hemisphere during the studied time interval, (3) gastropod faunas were concentrated in certain zones, based on which we have defined palaeobiogeographical provinces (table 2), and (4) most of the provinces except the one lying in the

Figure 2. Palaeobiogeographical distribution of the Eocene gastropods recorded in the Compendium (Sepkoski 2002). (1) Turridae, (2) Naticidae, (3) Epitoniidae, (4) Buccinidae, (5) Eight palaeobiogeographical provinces and similarities in generic composition between them.

subtropical part of the Southern Hemisphere share large number of genera.

3.1 Palaeobiogeographical provinces

The palaeobiogeographical provinces that are identified here based on concentration of gastropods in different regions of the world during the Paleocene (figure 1.5; table 2) are:

- Mediterranean Iranian Province (MIP) – the basins around the proto-Mediterranean including southern part of Europe, northern part of Africa and the Middle-East
- Middle European Province (MEP) – areas on the northeastern coast of Atlantic bordering Middle of Europe
- Greenland Province (GP) – Greenland
- Gulf Coastal Province (GCP) – The Gulf Coastal Plain, i.e., areas in USA surrounding the Gulf of Mexico
- Caribbean Northern South American Province (CNSAP) – Areas around the Caribbean sea including Caribbean archipelago and northern part of South America
- Western North American Province (WNAP) – The Pacific Coast of North America

Table 2. *Palaeobiogeographical provinces and their constituent countries.*

Serial no.	Province	Countries (States)
1	Mediterranean Iranian Province (MIP)	Spain, France, Italy, Bulgaria, Romania, the Russian Federation, Turkey, Croatia, Austria, Hungary, Greece, Somalia, Egypt, Saudi Arabia, Libya, Iraq
2	Gulf Coastal Province (GCP)	United States (Texas, Arkansas, Alabama, Tennessee, Louisiana, Mississippi, Georgia, Florida, North Carolina, South Carolina, Virginia, Maryland, New Jersey)
3	Caribbean Northern South American Province (CNSAP)	Columbia, Peru, Venezuela, Jamaica, Trinidad and Tobago, Panama, Haiti
4	Middle European Province (MEP)	United Kingdom, Netherlands, Belgium, Germany, Poland, Denmark, Norway, Sweden
5	Western Indian Province (WIP)	India, Pakistan
6	Western North American Province (WNAP)	United States (Oregon, Washington, California)
7	Indonesian Province (IP)	Indonesia
8	Greenland Province (GP)	Greenland
9	Nigerian Province (NP)	Nigeria
10	Austro-New Zealand Province (ANP)	New Zealand, Australia, Tonga

Table 3. *Provincialism of the Paleocene gastropod genera.*

		MIP	GCP	CNSAP	MEP	WIP	WNAP	GP	NP	ANP
Endemic genera	Number	23	40	4	47	5	6	12	6	29
	Percentage	19.33	29.41	16.67	25.68	13.16	16.67	10.9	12.24	55.77

Table 4. *Provincialism of the Eocene gastropod genera.*

		MIP	GCP	CNSAP	MEP	WIP	WNAP	IP	ANP
Endemic genera	Number	87	50	16	34	8	16	11	61
	Percentage	27.79	19.84	12.69	16.35	9.19	11.51	13.75	46.92

- Western Indian Province (WIP) – Western part of the Indian subcontinent including basins of Pakistan and western part of India
- Nigerian Province (NP) Nigeria – This tropical southern hemisphere area housed significant number of genera
- Austro-New Zealand Province (ANP) – Australia and New Zealand in the southern hemisphere are also found to bear high concentration of gastropod faunas.

Table 2 lists these provinces and their constituent countries.

Distribution of gastropod genera in the Eocene exhibits more or less similar pattern as in the Paleocene. However, there are a few noticeable differences. First, a considerable number of genera were recorded from the Indonesian archipelago during

the Eocene, whereas in the preceding epoch there was none. Hence, the Indonesian Province (IP) was established in the Eocene. Secondly, Greenland that housed a large fauna in the Paleocene lost all of it in the Eocene. Thus, GP ceased to exist in the Eocene. Finally, faunal diversity of NP of the Paleocene declined markedly in the Eocene. Because of much lower total number of genera during the Paleocene, generic concentration as low as 24 in a zone has been considered to define a province. However, for the Eocene having 639 genera, we have used 80 genera found in IP as the lower limit. Hence, the Nigerian Province has not been considered for the Eocene (table 2).

Palaeobiogeographical provinces, constituted of clusters of geographically proximal basins and separated from other such clusters, show significant generic endemism (tables 3 and 4). The ANP shows

Table 5. *Similarity matrix for the Paleocene showing number of genera in each province and generic similarity between the provinces expressed as percentage.*

	MIP	GCP	CNSAP	MEP	WIP	WNAP	GP	NP	ANP
MIP	119								
GCP	51	136							
	37.5%								
	42.85%								
CNSAP	10	16	24						
	41.66%	11.76%							
	8.40%	66.66%							
MEP	68	71	11	183					
	37.1%	38.79%	6.01%						
	57.1%	52.20%	45.83%						
WIP	19	17	4	24	38				
	50%	44.73%	10.52%	13.11%					
	15.96%	12.5%	16%	63.15%					
WNAP	10	22	5	17	10	36			
	27.77%	16.17%	13.88%	9.28%	26.31%				
	8.4%	61.11%	20.83%	47.22%	25.64%				
GP	41	28	8	76	8	13	109		
	37.61%	25.69%	7.34%	41.53%	7.34%	11.93%			
	34.45%	20.58%	33.33%	69.72%	21.05%	36.11%			
NP	23	25	7	27	18	7	16	49	
	46.93%	51.02%	14.28%	14.75%	36.73%	14.28%	14.81%		
	19.32%	18.38%	29.1%	55.10%	48.97%	19.4%	34.78%		
ANP	10	12	1	14	3	3	14	3	52
	18.86%	22.64%	1.88%	7.65%	5.66%	5.76%	12.72%	8.16%	
	8.4%	8.82%	4.16%	26.41%	7.89%	8.33%	26.92%	6.66%	

Table 6. *Similarity matrix for the Eocene showing number of genera in each province and generic similarity between the provinces expressed as percentage.*

	MIP	GCP	CNSAP	MEP	WIP	WNAP	IP	ANP
MIP	313							
GCP	119	252						
	47.22%							
	38.01%							
CNSAP	92	109	126					
	73.01%	86.50%						
	29.39%	43.25%						
MEP	150	131	91	208				
	72.11%	62.98%	44.23%					
	47.92%	51.98%	72.22%					
WIP	67	53	46	60	87			
	76.13%	60.22%	52.87%	28.86%				
	21.20%	21.03%	36.50%	68.96%				
WNAP	79	97	65	89	43	139		
	56.83%	69.78%	46.76%	42.78%	49.42%			
	25.23%	38.49%	51.58%	64.02%	30.93%			
IP	57	53	37	43	30	38	80	
	71.25%	66.25%	46.25%	20.67%	34.48%	45.23%		
	18.21%	20.94%	29.13%	53.75%	37.50%	27.74%		
ANP	49	47	25	50	18	38	12	130
	37.69%	36.15%	19.23%	24.03%	13.74%	29.23%	9.23%	
	15.65%	18.65%	19.84%	38.46%	20.68%	27.33%	15%

Figure 3. Column chart showing latitude-wise distribution of generic diversity in the Paleocene (1) and the Eocene (2).

Table 7. Latitudinal distribution of gastropod genera in the Paleocene and the Eocene along with extermination in the former and appearance in the latter.

		No. of genera	Extermination in Paleocene		Appearance in Eocene	
			No.	Percent	No.	Percent
Paleocene	<30°N	46	5	10.87		
	30°–50°N	297	42	14.14		
	>50°N	109	13	11.93		
	<30°S	68	3	4.41		
	30°–50°S	57	8	14.04		
	>50°S	19	3	15.79		
Eocene	<30°N	370			153	41.35
	30°–50°N	404			163	40.35
	>50°N	0			—	—
	<30°S	145			43	29.66
	30°–50°S	106			60	56.6
	>50°S	44			9	20.45

very high endemism. In other provinces the value varies from about 10 to about 30%.

Briggs (1974) introduced 10% specific endemism as the lower limit for an area to qualify as a biogeographical province. This criterion has been in vogue for the last over forty years proving its

stability and validity (Briggs and Bowen 2012). The present genus level study reveals generic endemism above 10% for all provinces except the WIP of the Eocene (tables 3 and 4). Any conservative extrapolation of the generic endemism values would put the specific endemism

Figure 4. Column diagram showing percentage of generic extermination in the Paleocene (1) and appearance in the Eocene (2) in different latitudinal divisions.

values for all the provinces including WIP much above 10%.

It is pertinent to mention that MIP was erected by Harzhauser *et al.* (2002), which included basins of northern Italy, Greece and central Iran, based on species level similarity of the Oligocene gastropods. Similarly, WIP was also erected on the same basis by Harzhauser (2007) for basins from the western Indian subcontinent. The Oligocene corals from Kutch have been designated to the same palaeobiogeographical unit, i.e., WIP (Sinha and Halder 2018). We here, propose identical palaeobiogeographical unit names for the Paleocene and the Eocene gastropods where distribution scenarios are

largely similar to that of the Oligocene such as MIP and WIP, to avoid multiplication of names for similar units. This way we acknowledge the fact that MIP and WIP were already taking their shape in the early Paleogene. Other province names are introduced here because formal palaeobiogeographical names for such areas of faunal concentration were not available.

3.2 Province relationships

3.2.1 Paleocene

Total number of Paleocene genera recorded in the Compendium (Sepkoski 2002) is 387 of which 325 continue in the Eocene. The similarity matrix for the Paleocene (table 5) and generic distribution of representative families like Turridae, Naticidae, Fasciolaridae and Buccinidae (figures 1.1–1.4) reveal high degree of faunal similarity among provinces of the northern hemisphere. Mediterranean Iranian Province (MIP) and Middle European Province (MEP), lying on the eastern margin of the Atlantic Ocean, share a lot of genera. Similarly, the two western Atlantic provinces – Gulf Coastal Province (GCP) and Caribbean Northern South American Province (CNSAP) – also show strong affinity. Interestingly, the western Atlantic provinces bear strong faunal resemblance across the ocean with the provinces of the eastern margin of the Atlantic (table 5). Western North American Province (WNAP), constituted of the Pacific coastal basins of North America, had maximum similarity with its geographically closest ally GCP, which lies on the Atlantic coast of the continent.

The Greenland Province (GP), the northernmost zone yielding a significant diversity of gastropod genera, appears to occupy a unique place among the northern hemisphere provinces. It had strong likeness only with the MEP but much less so with

Table 8. Change in latitudinal ranges of the genera from the Paleocene to the Eocene.

	No. of genera	Range extension to higher latitudes		Range extension to lower latitudes		Range remains unchanged		Range contraction	
		No.	Percent	No.	Percent	No.	Percent	No.	Percent
< 30°N	8	8	100	–	–	–	–	–	–
30°–50°N	170	43	25.29	90	52.94	14	8.24	23	13.53
>50°N	95	–	–	55	57.90	–	–	40	42.1
< 30°S	19	19	100	–	–	–	–	–	–
30°–50°S	16	4	25	6	37.5	5	31.25	1	6.25
>50°S	11	–	–	3	27.27	1	9.1	7	63.63

other palaeo-tropical and subtropical provinces (table 5; figure 1.5).

The Western Indian Province (WIP) shared 50 and 63.15% of its genera with MIP and MEP respectively (table 5; figure 1.5). MIP and MEP were constituted of basins surrounding the western part of the Tethys. MEP lay further north of MIP. Such huge similarity of WIP, which was still in the southern hemisphere during the Paleocene, with northern hemisphere provinces is interesting.

The Nigerian Province (NP), although lay in the southern hemisphere, also displayed conspicuous faunal affinity to the northern hemisphere provinces like MIP, MEP, GCP and WIP (table 5; figure 1.5).

The other southern hemisphere province ANP had much less similarity with any of the provinces (table 5; figure 1.5).

3.2.2 Eocene

Definition of the provinces and interprovincial relationships remained largely similar and became clearer in the Eocene. Gastropod diversity was much higher in this time than in the preceding epoch, and every province was characterized by more numerous genera (table 4). Northern hemisphere provinces revealed high interprovincial similarity (table 6; figure 2.5). About 45% or more similarity has been shown by all the province pairs of the Northern Hemisphere except that between Western Indian Province (WIP) and Indonesian Province (IP; table 6; figure 2.5). It may be pertinent to recall that WIP had moved in the northern hemisphere and IP was established in the Eocene. The maximum similarity occurred between the two western Atlantic provinces, i.e. Caribbean Northern South American Province (CNSAP) and Gulf Coastal Province (GCP). The two provinces to the east of Atlantic, i.e., Mediterranean Iranian Province (MIP) and Middle European Province (MEP), also bear very high faunal affinity (table 6; figure 2.5). The western Atlantic provinces exhibit very high similarity in generic composition across the ocean with the eastern Atlantic provinces in conformity with the pattern in the Paleocene. GCP shared 119 and 131 out of a total of 252 genera with MIP and MEP, respectively while CNSAP shared 92 and 91 out of 126, respectively with MIP and MEP (table 6; figure 2.5).

Western Indian basins (WIP) faunally resemble most MIP and MEP. Its similarity with western

Atlantic basins is also significantly high. WNAIP shows conspicuous similarity with western Atlantic as well as eastern Atlantic provinces. Its similarity was relatively less with WIP. IP, having relatively less recorded generic diversity in the Eocene, shows hefty similarity with western and eastern Atlantic provinces and WNAIP but relatively less with WIP (table 6; figure 2.5).

The only southern hemisphere province, Austro-New Zealand Province (ANP), had much less similarity with the northern hemisphere provinces (table 6; figure 2.5).

3.3 Latitudinal distribution

The latitude wise distribution of all the genera in the Paleocene and the Eocene exhibit much higher faunal diversity in the northern hemisphere than in the other (figure 3). Maximum faunal diversity lay within 30–50° latitudes in both the hemispheres and in both the epochs (figure 3). In the Paleocene 50–60°N latitudinal zone also recorded significant number of gastropod genera, which came from Greenland. Later, in the Eocene this zone was vacated. 20–30°N latitude, which was poorly represented in the Paleocene, recorded a large number of genera in the Eocene. In the southern hemisphere Antarctic basin recorded some genera in both the epochs, relatively more in the Eocene (figure 3).

The genera that did not continue from the Paleocene to the Eocene show roughly comparable rates of extermination from different latitudinal divisions except that below 30°S (table 7; figure 4.1). Fauna from the latter zone suffered much less extermination. The zone lying below 30°N latitude also recorded relatively less extermination. 30–50° latitudes in both the hemispheres saw relatively high rates of disappearance, which are comparable (table 7; figure 4.1). The genera that are recorded from Greenland also had representation in MEP and some other provinces. Hence, disappearance of GP after the Paleocene is not reflected in the percentage of generic extermination from latitudes beyond 50°N. All the Antarctic genera that were restricted to Paleocene were also restricted to that basin and went extinct.

Appearance of new genera in identical latitudinal divisions in the Eocene exhibits similar rates in the northern hemisphere (table 7; figure 4.2). Beyond 50°N latitude there was no recorded gastropod. 30–50°S zone records maximum new

genera whereas latitudes below 30°S saw fewer appearances. Antarctic basin also witnessed moderate degree of appearance (table 7; figure 4.2).

The genera that continued from the Paleocene to the Eocene were re-distributed during the latter epoch either by extension or contraction of their latitudinal ranges. Some generic ranges remained unchanged (table 8). All the lower latitude faunas extended their ranges towards higher latitudes. The fauna that thrived within 30–50° latitudes in the two hemispheres exhibited a more pronounced tendency of range extension towards lower latitudes than towards higher latitudes. Range contraction is most pronounced for Greenland and Antarctic faunas. However Greenland faunas also made a considerable range extension towards south (table 8). It may be pertinent to remember that a large proportion of the Greenland fauna was already present in relatively lower latitudes.

4. Discussion

4.1 Province relationship and disposition of land and sea

The distribution of gastropods in the Paleocene and the Eocene was concentrated in many shallow basins mainly of the northern hemisphere (figures 1–3). The reconstructed palaeo-coastline maps (Smith *et al.* 1994) display that in the northern hemisphere, especially in Europe, there were many small land masses surrounded by and also enclosing small shallow water bodies. Overall land area with ocean around the large continents was also higher in the northern hemisphere than in the southern hemisphere. So, shallow benthic area including open oceans around the continents and epicontinental basins was much greater in the northern hemisphere than in the southern hemisphere. Shallow benthic zone has always been the most populated area because of the presence of all favorable ecological factors such as light, food and oxygen. Shallow benthic gastropod faunas, hence, flourished in a big way in the northern hemisphere. Provinces such as the Mediterranean Iranian Province, the Middle European Province and the Gulf Coastal Province had maximum concentration of generic diversity. Apparently, large areas of shallow benthic habitat were available in these zones (see maps 6–9, Smith *et al.* 1994) that encouraged diversification.

The provinces exhibited considerable endemism (tables 3 and 4). Endemism of the ANP is, however, significantly higher than that of others. This province obviously had much less affinity with other contemporaneous provinces. All the provinces except ANP shared much more of their faunas than their endemic components. These provinces lay along palaeo-tropics and subtropics mainly of the northern hemisphere. This distribution pattern of the gastropods during the Paleogene is reminiscent of the Mesozoic distribution of marine faunas in the Tethys Realm. It appears that this palaeobiogeographical unit continued to exist in the Paleogene with some modifications although the Tethys Ocean had disappeared.

Very high faunal similarities between the Mediterranean Iranian Province and the Middle European Province, and between the Gulf Coastal Province and the Caribbean Northern South American Province (tables 5 and 6) reflect their geographical proximity. But the two former provinces of eastern Atlantic were separated by the Atlantic Ocean from the latter two western Atlantic Provinces but their faunal similarity is remarkable. This indicates there was a trans-Atlantic current that propelled and carried the planktonic larvae of these benthic organisms. Harzhauser *et al.* (2002) arrived at a similar conclusion after analyzing distribution of the Oligocene gastropods. They also thought that the current was from east to west carrying larvae from MIP towards the west coast of Atlantic. In the present study, we did not attempt to delineate the direction of migration of organisms. However, Givens (1989) recorded typical Tethyan molluscs including 32 gastropod genera and 14 bivalve genera to have migrated to the Gulf Coastal Plain during the Eocene. He (Givens 1991) also depicted fortuitous dispersal of *Lyrischapa*, a Tethyan gastropod genus belonging to the family Volutidae, to the Gulf Coastal Plain with the help of westward moving Tethys Palaeocurrent (Haq 1981). It may be pertinent to mention here that today major westward surface currents carry eastern Atlantic marine fauna to the west across the Mid-Atlantic barrier, thereby developing some resemblance between western Europe and eastern America (Silva *et al.* 2014). However, the issue about the direction of migration of the recent larvae is far from resolved. Phylogenetic reconstruction of *Felimare picta* complex, a nudibranch gastropod group that occurs on both sides of the Atlantic, does not match with this westward migration hypothesis. Hence, alternative

hypothesis of eastward migration facilitated by eastward currents such as the Gulf Stream and equatorial counter current has been proposed (Almada *et al.* 2016).

The Indian subcontinent was in the southern hemisphere in the Paleocene and moved to the northern hemisphere during the Eocene (figures 1 and 2). This movement apparently did not alter its palaeobiogeographical affinity. It shows maximum similarity to MIP throughout the Paleocene and the Eocene (tables 5 and 6) although the number of genera for the Paleocene is poor. The high similarity the western Indian Province shows with MIP (tables 5 and 6) signifies regular connection between these two provinces. The proto-Mediterranean Sea lying between Europe to the north, Africa to the south and Indian subcontinent to the east during the Paleogene apparently provided the sea route for this connection. Harzhauser *et al.* (2002), following Popov (1993), demonstrated an easterly surface current from the Mediterranean part of Europe during the late Eocene that bathed the shores of the western Indian subcontinent. WIP might have received faunal components from the MIP, if a similar current was there during earlier part of the Paleogene. Iqbal (1969a, b, 1972) noticed that several Paleogene western Indian (Pakistan) mollusc species were discovered from the Mediterranean Europe from relatively younger stratigraphic levels. However, he refrained from explaining it by westward migration from Indian side to the Mediterranean in the absence of any more authentic evidence. In this study, we did not attempt to elucidate any direction of migration. High faunal similarity of WIP with MEP (tables 5 and 6) was apparently through MIP. The same holds for its similarity with the western Atlantic provinces, i.e., CNSAP and GCP (tables 5 and 6). WIP showing less similarity with CNSAP during the Paleocene is perhaps attributable to the fact that both these provinces were characterized by low faunal diversity.

The Western North American Province lying on the Pacific coast of North America should have connection with CNSAP and also GCP via the shallow sea route between the Americas (figures 1.5 and 2.5). This connection was severed much later during the Pliocene with the development of Isthmus of Panama. The data (tables 5 and 6) support this contention. During the Paleocene WNAP, however, exhibited less similarity with CNSAP (table 5). Generic diversity of both these provinces for the Paleocene were low. Hence, this low faunal

affinity may not reflect their actual biogeographical closeness, which became pronounced in the succeeding epoch. Low diversity of WNAP and WIP during the Paleocene is also reflected in the low faunal affinity between these provinces (table 5). In the Eocene this relationship was also strengthened (table 6). In the Eocene, when WNAP had a diverse gastropod fauna, its relationship with other provinces became clearer. High similarity of WNAP with eastern Atlantic provinces and also with WIP (table 6; figure 2.5) can be explained by prevailing trans-Atlantic current and current along the relict Tethyan seaway.

Greenland Province of the Paleocene, which disappeared in the Eocene, had much higher similarity with MEP than with any other province (table 5). The province sharing maximum similarity with the closest geographical neighbor is not surprising. However, much lower affinity of GP with other contemporaneous provinces is noteworthy in contrast to generally quite high interprovincial similarity that prevailed during this time. High latitudinal position of the province acted as filter for many genera and allowed only relatively cold-tolerant genera from the latitudinally closest province, i.e., MEP (figure 1), to reach the shores of Greenland. In the Eocene, Greenland moved northward and lost its gastropod fauna (figure 2).

The Nigerian Province had direct connection with the proto-Mediterranean through a narrow NE-SW directed strait across western Africa during the Paleocene (see Map 9, Smith *et al.* 1994; see also Adegoke 1972, 1977). This strait disappeared in the Eocene severing the link (see Map 6–8, Smith *et al.* 1994). Presence of the link in the Paleocene and its disappearance in the Eocene are clearly related to the appearance and the disappearance of NP. Strong faunal similarity of NP with all genus-rich provinces of the northern hemisphere vindicates its link through the epicontinental strait. A genus-poor fauna (total number of genera 39) continued in this area in the Eocene that did not qualify for consideration of a province.

A total of 80 genera have been recorded from the Indonesian Province, which lay on the western Pacific and appeared only in the Eocene. It also displays high faunal similarity with almost all the northern hemisphere provinces in the Eocene. However, its similarity with WIP is relatively less. Strong similarity of IP with GCP, CNSAP, MIP and MEP, and relatively less with WIP (table 6) indicate that the larvae dispersed mainly along the Pacific. However, this extremely long distance of

deep ocean water is a huge barrier to dispersal. It is impossible to cross this barrier with the surface current without several shallow hopping stations. While IP raises an interesting question regarding dispersal it vindicates the presence of a tropical–subtropical fauna around the globe, much like the Tethys Realm fauna in the Mesozoic.

The only southern hemisphere province, the Austro-New Zealand Province, also lay in the tropical–subtropical zone. Climatic control is obvious from such distribution. ANP had much less similarity with any of the northern hemisphere provinces (tables 5 and 6; figures 1.5 and 2.5) and very high endemism (tables 3 and 4). These indicate presence of a strong barrier to dispersal extended in east–west direction roughly paralleling the equator during the Paleogene. Presence of large deep ocean water separating this province from all the northern hemisphere provinces and perhaps also ocean currents in this direction and absence of any across it, acted as strong barriers.

4.2 Role of climate and thermal maxima on diversity and distribution

The distribution of gastropods of the Paleocene and the Eocene was primarily restricted to palaeotropics and subtropics, with only a few extended to higher latitudes. This restriction indicates a strong control of temperature on their distribution. Disappearance of the Greenland fauna with the northward shift of the landmass in the Eocene also attests to the temperature sensitivity of this benthic organism. However, the presence of a significant number of genera well beyond 30° latitudes on both hemispheres indicates warmer and more equable climate during the Paleocene–Eocene than the present day. It is generally believed that the earth entered the present icehouse stage only in the Oligocene when polar ice cap started to develop (Zachos *et al.* 2006, 2008; Harding 2010; Hansen *et al.* 2013). With cooling climatic zonation became more pronounced.

The fact that temperature imposed a very significant control on the distribution of benthic fauna has also been demonstrated by other organisms such as the Cenozoic corbulid bivalves (family Corbulidae) (Halder and Bano 2015), the Eocene cerithioid gastropods (superfamily Cerithioidea) (Halder and Sinha 2014) and the Oligocene corals (Sinha and Halder 2018). Interestingly, nektonic nautiloids also exhibited a similar pattern (Halder 2012) demonstrating control of temperature.

Gastropod diversity of the Paleocene was relatively low. This perhaps reflects lull after the huge catastrophe at the end of the Mesozoic. This diversity further decreased by the extinction of about 16% of the gastropod genera in the Paleocene. Rate of extermination in the Paleocene in different latitudinal zones remain roughly similar with slight tendency of increase towards higher latitudes (table 7; figure 4.1). Extinction of higher latitude faunas has been documented and explained as a response to the sudden increase in global temperature at the Paleocene–Eocene boundary phenomenon PETM (see Samanta *et al.* 2013 and references therein). This is expected because in a global warming event, organisms optimally adapted at low temperatures would cease to get their favorable climate. The lower latitude faunas, in such a situation, generally exhibit a tendency to move towards higher latitudes in search of a temperature they were optimally adapted to. All the low latitude (less than 30° in both the hemispheres) gastropod genera that continued from the Paleocene to the Eocene show a clear tendency of range extension towards higher latitudes in the latter epoch (table 8). It may be pertinent to note that significant extermination also occurred in the low latitudes except in the southern hemisphere. This record is important because it is generally believed that low latitudes were not greatly affected in the PETM (see Samanta *et al.* 2013).

While the Paleocene saw a considerable fall in diversity the diversification that followed in the Eocene was much more pronounced (table 1). The diversification mostly occurred in low to mid-latitude zones (>30 to <50°) (table 7; figure 4.2). The Paleocene–Eocene boundary deposits from many areas in the world including Tethyan basins record conspicuous evidences of transgression (e.g., Speijer and Morsi 2002; Sluijs *et al.* 2008, 2011, 2014; Schulte *et al.* 2011; Pujalte *et al.* 2014). Opinions differ as to whether such transgressions are a response to PETM and other early Eocene thermal events. Indian subcontinent also witnessed transgression during early to middle Eocene, in response to which marine foraminiferal limestones were deposited in extensive areas near present day coasts. These transgressions and hence, development of extensive shallow shelves were responsible for the remarkable diversification in the Eocene. The mid-latitude (30–50°) gastropod faunas that persisted since the Paleocene show a greater tendency of extending their ranges towards

relatively lower latitudes than towards higher latitudes (table 8). The high-latitude faunas ($>50^\circ$) also exhibit range extension towards lower latitudes along with considerable range contraction (table 8). These are somewhat perplexing and difficult to explain considering global warming due to PETM and early Eocene hyperthermal events. At the present state of knowledge it appears, the effect of transgression overwhelmed that of warming in this dispersal towards lower latitudes.

5. Conclusion

Generic distribution of the Paleogene gastropods depicts presence of a truly cosmopolitan biota around the world in tropical and subtropical belts, primarily of the northern hemisphere. Low latitude Tethys Realm of the Mesozoic appears to continue in the Paleogene in a modified and much widened configuration. Along with basins from southern Europe, Middle East, northern Africa and western Indian subcontinent the realm in the Eocene accommodates Central American and Caribbean basins, Gulf Coastal Plain, parts of western North America and Indonesian Archipelago. In consideration of its significant difference in size, shape and province composition from its Mesozoic counterpart, and absence of Tethys Ocean in the Paleogene we, here, propose to erect a new realm, namely Northern Tropical Realm.

Presence of an essentially similar fauna around the world evinces presence of oceanic surface currents along east–west such as the trans-Atlantic, the proto-Mediterranean and perhaps also the Pacific. Such currents acted as barriers to dispersal for north–south movement of planktotrophic larvae of these benthic organisms. The currents along with intervening wide, deep ocean basins separated Austro-New Zealand Province from the Northern Tropical Realm and promoted independent evolution of the fauna in the former.

Temperature was a major control in the gastropod distribution. It is evidenced by restriction of the distribution mainly within palaeo-tropics and subtropics. Hyperthermal events at the Paleocene–Eocene boundary and in the early Eocene were responsible for dispersal of low-latitude faunas to higher latitudes and relatively higher extinction of high-latitude faunas. Contemporaneous transgression in the mid- and low-latitude basins,

however, facilitated diversification and countered the effect of hyperthermal events.

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