

Some aspects of the palaeobiology of Tertiary deep-Sea Ostracoda from the S.W. Pacific

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ABSTRACT—From a numerical analysis of deep water Neogene and Quaternary Ostracoda from D.S.D.P. sites in the S.W. Pacific, it is shown that the Miocene to Quaternary interval saw a large scale invasion by bathyal stocks of the abyss. This invasion was progressive and cumulative and resulted in abyssal faunas being much more diverse in the Quaternary than they had been in the Miocene. This major palaeoecological shift also occasioned a concomitant decline in bathyal faunas over the same interval. The breakdown of bathyal and abyssal isolation resulted from the Miocene onwards, in a progressive increase in the number of species which were able, contemporaneously, to live at both bathyal and abyssal palaeodepths.

The study shows deep water faunas of this age to be much more diverse than previous studies have indicated. Ninety-one genera with autochthonous deep water species are encountered in this study. These genera are listed with the numbers of species of each genus and their depth distribution for Miocene, Pliocene and Quaternary respectively. Overall species diversity declines from the Miocene to the Pliocene but steeply increases into the Quaternary. It is suggested that the Pliocene impoverishment may in part be an artefact, occasioned by abnormally high Miocene diversity.

It is shown that the phenomena outlined above are, to varying degrees, illustrated by all of the 6 groups into which the fauna is divided. It is suggested that certain of these phenomena, such as the major downslope migration from the Miocene onwards, may be detectable in other parts of the world's oceans.

INTRODUCTION

This paper presents some of the results of a study being undertaken at Aberystwyth into Upper Cretaceous to Recent deep sea benthonic Ostracoda. Material has been examined from all of the world's oceans but with particular emphasis on the North Atlantic and S.W. Pacific Oceans. The present paper is a compilation of some of the results obtained from the Neogene and Quaternary of the latter area and, while incorporating some additional data, conforms in all major respects to the address given by the author to the British Micropalaeontological Society on 17th November 1982.

The aim of the project is to conduct, for the first time, a detailed and comprehensive study of the entire benthonic ostracod fauna in order to promote a better understanding of its origins, taxonomic composition, evolution, palaeoecology and palaeobiology. The achievement of these aims has been in some measure frustrated by the very newness of the fauna. A very high percentage of the species and not a few genera are new and this has necessitated a large initial emphasis on descriptive work. Despite this, considerable progress has been made in a number of areas.

Although much of our knowledge of Recent deep sea Ostracoda is still based upon the results of the Challenger Expedition (Brady, 1880; Puri & Hulings, 1976) a

growing number of studies on deep sea Tertiary and Recent Ostracoda have appeared in Recent years. Among these are: Benson, 1969, 1971, 1972a, b, 1974, 1975, 1976, 1977, 1978, 1982; Benson & Sylvester-Bradley, 1971; Ducasse & Peypouquet, 1979; Joy & Clark, 1977; Malz, 1981; Peypouquet, 1975, 1977, 1979; Steineck, 1981; Swain, 1970a, b; Whatley *et al.*, 1982, in press a, b, c.

A major deficiency of many of these contributions has been their somewhat select nature. For example, Benson, the major contributor to these studies has largely concentrated on a single family of ornate Ostracoda, the Trachyleberididae, to support his theories on global palaeoceanography and the evolution of carapace architecture etc. Similarly, Peypouquet has been primarily concerned with demonstrating the potential of two genera, *Krithe* and *Parakrithe*, as palaeoenvironmental and particularly depth indicators.

As a consequence of these studies, any student reading the literature on Tertiary and Recent deep sea ostracod faunas could be forgiven for concluding that the generic and specific diversity of these faunas was very low. How wrong they will be! This paper demonstrates that deep sea ostracod faunas are much more diverse than prior studies would indicate.

The deep sea environment is a complex mixture of the hostile and the benign. On the one hand, since about the end of the Eocene it has been very cold. Abyssal temperatures range from 0°–4°C and bathyal temperatures from 4°–7° or 8°C. There is no light, pressure is high and the threat of dissolution of shell material is never far away at abyssal depths. On the other hand, there is great stability. There are no diurnal nor seasonal variations in temperature, light or salinity etc. There are high concentrations of nutrient salts, particularly nitrates and phosphates and oxygen is plentiful. Energy levels are generally low and a food supply exists in the continual rain of dead plankton.

In the main, the virtues seem to outweigh the disadvantages. Certainly, large numbers of different animals of very diverse morphology and mode of life live at these depths, not least among them the Ostracoda.

Most of the micropalaeontological effort associated with the D.S.D.P. programme has been devoted to the study of pelagic microfossils. One intention of this paper is to promote greater micropalaeontological interest in the benthos.

LOCATION OF THE STUDY AREA

The study is based on a total of 156 samples from 19 D.S.D.P. sites and 5 samples of Miocene age collected by a French Expedition in the Loyalty Basin. The location of the sites and an indication of their gross stratigraphy is

given in Fig. 1 and further data is given in Table 1.

In Fig. 1, drawn on the bathymetric map, is a line separating a Northern "Abyssal" Province and a Southern "Bathyal" Province. Palaeodepths between 1000 m and 2000 m are referred to as bathyal and those greater than 2000 m as abyssal.

The most important D.S.D.P. sites in the Southern "Bathyal" Province are Site 209, on the Queensland Plateau and Sites 208, 207 and 284 on the Lord Howe rise. These sites have been continuously sampled throughout the Tertiary and Quaternary. During the Palaeocene and early Eocene, these sites were at outer shelf depths and many of the species had eyes and the fauna includes such warm water indications as *Cytherelloidea* as dominants. The Queensland Plateau and Lord Howe Rise, through the later Palaeogene slowly subsided to the bathyal depths (1300–1500 m) which were achieved by the Miocene (Burns & Andrews, 1973; Packham & Andrews, 1975). From the late Palaeogene, ostracod faunas at these sites contain no sighted species and *Cytherelloidea*, for example, is absent.

To the N. and N.E. of the line the sites we have studied were probably at abyssal depths for most or all of the Tertiary. In these we find a distinct fauna of abyssal character from which genera such as *Cytherelloidea* were always excluded, as were sighted species.

The only guyot we have studied is situated in the Northern Abyssal Province. The summit of this flat-

Table 1. The D.S.D.P. sites: their location, present day water depth and age of samples.

	Site	Systems studied	Present day water depth	Lat.	Long.
Bathyal	277	Quaternary	1214 m	52° 13.43' S	166° 11.48' E
	281	Quaternary	1591 m	47° 59.84' S	147° 45.85' E
	284	Quaternary	1066 m	40° 30.48' S	167° 40.81' E
	207	Neogene to Quaternary	1389 m	36° 57.75' S	165° 26.06' E
	208	Neogene to Quaternary	1545 m	26° 06.61' S	161° 13.27' E
	209	Neogene to Quaternary	1428 m	15° 56.19' S	152° 11.27' E
Abyssal	282	Quaternary	4202 m	42° 14.67' S	143° 29.18' E
	279	Quaternary	3341 m	51° 20.14' S	162° 38.10' E
	206	Pliocene to Quaternary	3196 m	32° 00.75' S	165° 27.15' E
	262	Quaternary	2298 m	10° 52.19' S	123° 50.78' E
	288	Neogene	3000 m	5° 38.35' S	161° 41.53' E
	289	Neogene to Quaternary	2206 m	0° 29.92' S	158° 30.69' E
	62	Neogene	2591 m	10° 52.2' N	141° 56.3' E
	64	Neogene to Quaternary	2052 m	1° 44.4' N	158° 36.54' E
	55	Neogene	2850 m	9° 18.1' N	142° 32.1' E
	56	Miocene	2508 m	8° 22.4' N	143° 33.6' E
Guyot	57	Pliocene	3300 m	8° 40' N	143° 32.0' E
	47	Pliocene	2689 m	32° 27' N	157° 43' E
	200	Neogene	1469 m	12° 50.2' N	156° 47.0' E

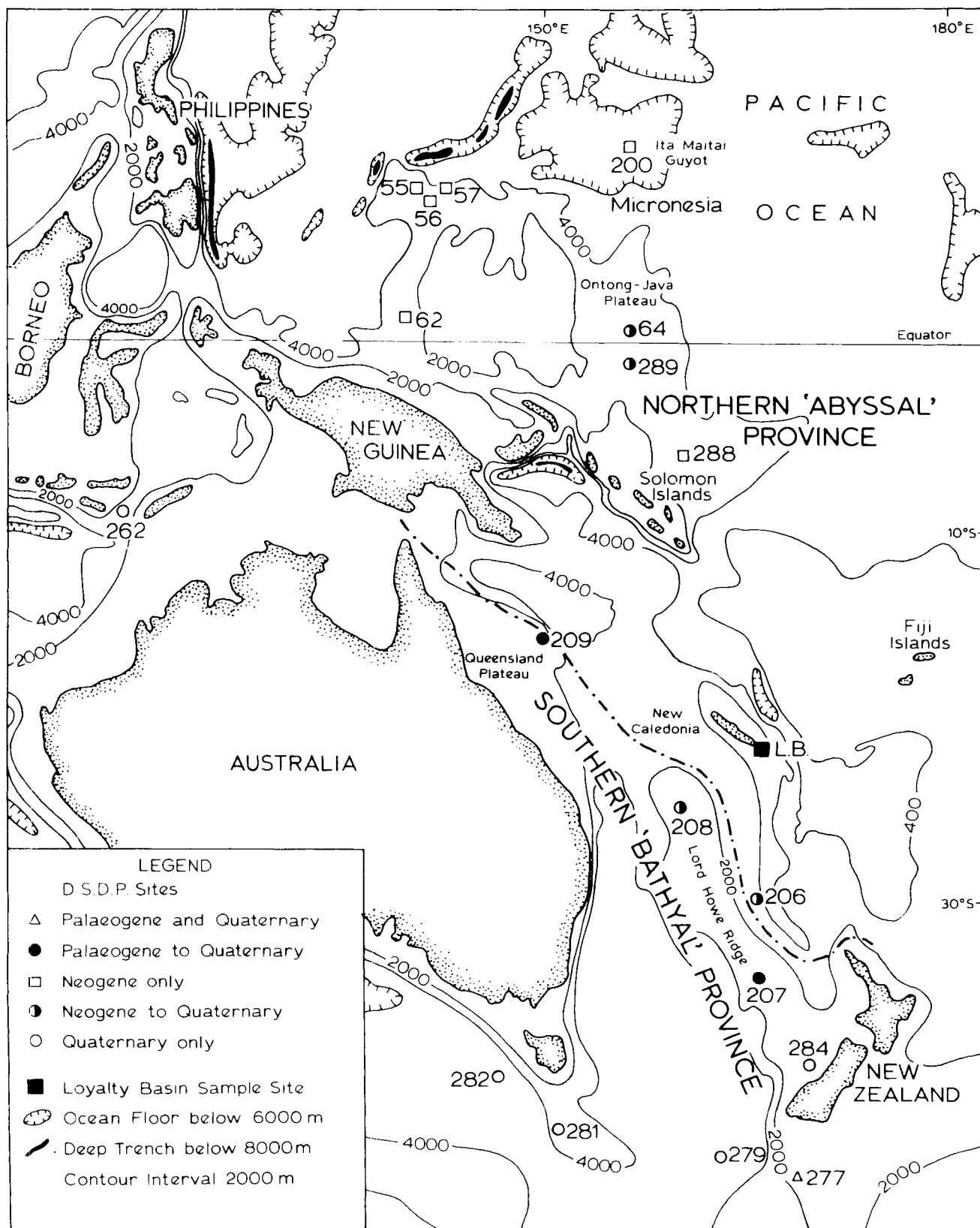


Fig. 1. Bathymetric map of S.W. Pacific with D.S.D.P. sites and their gross stratigraphy.

Table 2. The Stratigraphical and depth distribution of the fauna. B = Bathyal, A = Abyssal

Genera	MIOCENE				PLIOCENE				QUATERNARY			
	Total No. spp.	No. B. spp.	No. B + A. spp.	No. A. spp.	Total No. spp.	No. B. spp.	No. B + A. spp.	No. A. spp.	Total No. spp.	No. B. spp.	No. B + A. spp.	No. A. spp.
GROUP 1												
Cardobairdia	1	1										
Neonesidae	1	1			2		2		5	2	1	2
Paranesidea	1			1								
Bairdoppilata	3	2		1	3	2		1	3	1	1	1
Bythocypris	6	5		1	2	2			14	4	1	9
Zabythocypris	1	1			3	2	1		3	1	2	
Macrocypria	1	1										
Propontocypris	2	2			1	1			7	2		5
Cyprid gen. nov.	3	2		1	1	1			2	2		
Argilloecia	17	11	1	5	11	9	2		21	9	5	7
Australoecia	4	1	1	2	3	3			15	9	1	5
Abyssocypris	5	2		3	1			1	2	1		2
Paracypris	1	1			1	1			5	3		2
Anchistrocles									4	1		3
Macrocypria									3	1	1	1
GROUP 2												
Krithe	43	25		18	43	26		17	54	20	15	19
Parakrithe	3	1		2	2	1		1	5	1		4
GROUP 3												
Bythocytheromorpha	2	2										
Cretaceratina	1	1										
Cytheralison	4	4			1	1			1	1		
Pseudoloxoconcha	2	2										
Gen. nov. 1	2	2							1			1
Indet. gen. 1	1	1										
Bythocythere					1	1			9	2		7
Bythoceratina					3	3			4	3		1
Gen. nov. 2					1	1			1		1	
Pseudocythere									9	3		6
Phlyctobythocythere									1	1		
Orientocythere									1			1
Indet. gen. 2									1	1		
GROUP 4												
Eucythere	18	14	1	3	12	11	1		14	10	2	2
Cytheropteron	30	22	2	6	31	26	2	3	57	23	12	22
Aversoalva	9	8		1	13	8		5	10	4	3	3
Eucytherura	13	8	4	1	4	3	1		8	6	1	1
GROUP 5												
Bradleya	12	10	1	1	7	5	1	1	13	6	2	5
Quasibradleya	1	1										
Poseidonamicus	4	3	1		6	1	3	2	7	3	3	1
"Trachyleberis"	1	1										

Tertiary deep-sea Ostracoda

Actinocythereis	2	1	1									
Acanthocythereis	3	3			1	1						
Gen. nov.	2	2			1	1			3	3		
Atlanticythere	1		1									
Abyssocythere	1			1	3			3	1		1	
Henryhowella	3	1		2	6	1	1	4	4		4	
Echinocythereis	1	1							2		2	
Toolongella	1	1			1	1						
Indet. gen. 1	1	1										
Indet. gen. 2	1	1										
Indet. gen. 3	1	1										
Indet. gen. 4	1	1										
Indet. gen. 5	1	1										
Indet. gen. 6	1	1										
Indet. gen. 7	1	1										
Agrenocythere					1			1	1			1
Ambocythere					6	2	1	3	2	1		1
Cletocythereis					1	1						
“Thalassocythere”					1		1		8	5	1	2
Indet. gen. 8					1		1					
Indet. gen. 9					1		1					
Indet. gen. 10					1			1				
Indet. gen. 11					1	1						
Indet. gen. 12					1		1					
“Oxocythereis”									3	1	2	
Phacorhabdotus									2			2
Indet. gen. 13									6	4		2
Indet. gen. 14									3		3	
Indet. gen. 15									1		1	1
Indet. gen. 16									1		1	
<hr/>												
GROUP 6												
Saida	2	2							3	1		2
Bosquetina	1			1	1			1	2		1	1
Rockallia	1		1		1		1		3	1	1	1
Typhlocythere	1	1			1	1			2	1		1
?Semicytherura	1	1										
Paracytheridea	1			1								
Pedicythere	1	1			2	2			3	2	1	
Swainocythere	1	1										
Pelecocythere	1		1		2	1	1		5	3		2
Loxoconcha	1		1		1	1						
Indet. gen.	1	1										
Abyssocythereis	1			1	1			1				
Xestoleberis	5	4		1	4	4			4		1	3
Cytherella	4	2	1	1	3	1		2	6	1	1	4
Cytherelloidea	2	2										
Polycope	3	3							4			4
Copytus					2	2			1			1
Hemicytherura					1	1						
Cluthia					1	1			1	1		
Paijenborchella					1	1			5	1		4
Cytherura									1	1		
Paradoxostoma									5	3		2
Manawa									1			1

topped seamount, the Ita Mai Tai Guyot, was throughout most, if not all of the Tertiary, at some 1400 m but was, and is, surrounded on all sides by an abyssal plain at some 6000 m.

COMPOSITION OF THE FAUNA

With the exception of detailed studies on such genera as *Rockallia*, *Bradleya* and *Poseidonamicus* (Whatley *et al.*, 1981, Whatley *et al.*, in press a, b, c). Our studies on the Palaeogene of the area are incomplete and since numerical data are not yet available for the early Tertiary, this paper will be restricted to a consideration of faunas and events in the Neogene and Quaternary.

In the Neogene and Quaternary we have encountered 91 genera. Their gross depth distribution and the number

Quaternary	365 species	58 genera	12 DSDP sites	52 samples
Pliocene	200 species	50 genera	12 DSDP sites	61 samples
Miocene	238 species	62 genera	10 DSDP sites	48 samples
+ Loyalty Basin				

The decline in the number of taxa, particularly species, from Miocene to Pliocene is well shown in Fig. 2 as is the steep increase in the number of species into the Quaternary. The reasons for this Pliocene impoverishment are not easily found and the author knows of no parallel among other Pliocene faunas. Indeed, the specific diversity of the Upper Pliocene of Cornwall and N.W. France is approximately 600; greater than any previously known ostracod fauna (Maybury verb. comm. 1983). Similarly, it is difficult to equate this phenomenon to climatic deterioration since benthonic faunas should be largely insulated from this and also because of the pronounced enhancement of diversity in the same area during the Quaternary.

Possibly the answer will be more readily discernable when the data for the Palaeogene is available. This may demonstrate that the apparent Pliocene "low" is, in fact, due to a Miocene "high". This may have been in response to global climatic and oceanographic events (Savin *et al.*, 1975; Shackleton & Kennett, 1975a, b; Moore, Pisias & Keigwin, 1981). Evidence of enhanced diversity of *Bradleya* and *Poseidonamicus* in the Miocene of the same area (Whatley *et al.*, in press a, b, c) may be confirmatory evidence of this.

The Neogene and Quaternary deep water fauna of this region is very distinctive in its composition. Many elements which on contemporary shelf seas in the same area are dominants (Swanson, 1969; Hornibrook, 1952; McKenzie, 1974; Kingma, 1948; Keij, 1979, a, b; Whatley & Downing, in press) are absent in the deep water facies or occur in very reduced circumstances. Among these, for example, are loxoconchids, leptocytherids pectocytherids, paradoxostomatids hemicytherids, leptocytherids, xestoleberids, many groups of cytherurids and some bairdiaceans. As yet unpublished work in the northern Indian Ocean and North Atlantic

of species of each genus occurring in the Miocene, Pliocene and Quaternary of the area is given in Table 2. The number of species in each of these divisions which are confined to bathyal or abyssal palaeodepths and those which occur in both are also given. Genera to be described in due course as new are deliberately left in open nomenclature. Many of the unidentified genera are new but lack sufficient material to allow them to be so designated.

The list of genera are presented under 6 group headings which will be explained below. In this list and in subsequent Figs., species from the Ita Mai Tai Guyot are treated as bathyal.

Gross statistics on the faunas are as follows:

confirms this clear distinction between Neogene and Quaternary deep water and shelf faunas.

Krithe is the dominant genus in virtually every sample and is very diverse. Marine cyprids, particularly *Argilloecia* are also very diverse and bairdiaceans are quite diverse.

The Bythocytheridae are somewhat patchy in both depth and stratigraphical distribution but are moderately diverse taken overall. *Eucythere* (s.s. and the subgenus *Rotundracythere*), *Cytheropteron*, *Aversovalva* (which we have good evidence to consider as a distinct genus) and *Eucytherura* are all very diverse, particularly *Cytheropteron* which is second only to *Krithe*.

The Trachyleberididae are, as a family, very diverse; particularly *Bradleya* and *Poseidonamicus*.

Other forms which are not diverse nor often abundant, occur consistently and are very characteristic of Neogene to Recent faunas worldwide. They include such genera as *Saida*, *Rockallia* and *Pelecocythere*.

Curiosities among the fauna include the abyssal genus *Abyssocythereis*, a survivor of the essentially late Mesozoic Protocytheridae. Other Mesozoic relicts are such genera as *Toolongella* originally described from the Upper Cretaceous of Western Australia by Bate (1972) and which survives in bathyal palaeodepths to the Pliocene. Similarly, *Cretaceratina trispinosa* Neale, 1975 survives on the Ita Mai Tai Guyot to the Miocene.

A single specimen of a new species of the palaeocopid genus *Manawa* has been encountered in the Quaternary and a distinct species group of the normally phytal genus *Xestoleberis* occurs at both bathyal and abyssal palaeodepths. The author has seen similar species in the Quaternary of the North Atlantic at similar palaeodepths.

Throughout this study I have carefully distinguished between autochthonous and allochthonous elements. Many of the latter are familiar from personal studies of

shelf forms or from a study of the literature. Species are considered to be autochthonous by virtue of high incidence and an appropriate population age structure. More than 100 species have been rejected as allochthonous, mainly in the Quaternary.

ORIGINS OF THE FAUNA

Until the data on the Palaeogene fauna is available, it is not possible to provide precise evidence for the origins of the Neogene fauna. However, it can be shown to comprise two distinct components:

1. Forms which had entered the deep sea prior to the Miocene; some perhaps as early as the Cretaceous. By the Miocene (and probably earlier) the members of this group are more or less regularly distributed throughout both bathyal and abyssal environments. *Krithe* is one such example (Table 2). In the Miocene, this genus is almost equally diverse at all of the 11 DSDP sites, bathyal and abyssal, although overall there are more bathyal than abyssal species.

2. Forms which entered the deep sea later than those of group 1 (probably late Palaeogene) and which, in the Miocene are much more bathyal than abyssal in their depth distribution. Elsewhere it has been shown that *Bradleya* and *Poseidonamicus* are good examples of this group (Whatley *et al.*, in press a, b, c). Table 2 also illustrates this phenomenon with respect to these two genera and also others, such as *Cytheropteron*, *Argilloecia* and many more. Many genera in this group, however, in the interval Miocene to Quaternary illustrate a major downslope migration into the abyss e.g. *Cytheropteron*.

Whatley *et al.* (in press a, b, c) have shown by detailed studies of various lineages of *Bradleya* and *Poseidonamicus* throughout the Tertiary that this region is an important locus for induction into the deep sea. This was caused by the previously mentioned subsidence of the area between Australia and New Zealand during the Palaeogene at a rate slow enough for elements of the fauna to adjust and to survive. This subsidence brought elements of shelf faunas involuntarily down to bathyal depths by the late Palaeogene. In due course, this newly established bathyal fauna migrated outwards from this locus into deeper water. Although this migration probably also occurred into abyssal depths to the south, we are only able to document it into the Northern "Abyssal" Province.

THE MIOCENE TO QUATERNARY INVASION OF THE ABYSS

An examination of the depth distribution of Miocene to Quaternary deep water Ostracoda in the S.W. Pacific (Fig. 3) shows an increase, with time, in the number of bathyal species which enter the abyssal realm. It also shows an overall decline in the number and percentage of bathyal species and complementary increases in the

number of species confined to abyssal palaeodepths. Notwithstanding this major ecological shift, bathyal only species, by both total number and percentage, dominate the deep water fauna. However, by the Quaternary the progressive occupation of the abyss has resulted in near parity in bathyal and abyssal specific diversity. This change from the difference in diversity between the two realms in the Miocene is dramatic as is the progressive increase in the number of species which are encountered in both realms, particularly from the Pliocene onwards. In Fig. 3 and in many instances in Figs. 4–8, the graphs clearly reflect the apparent impoverishment of the Pliocene.

Fig. 4 illustrates the number and percentage of genera which are confined to bathyal and abyssal palaeodepths and also those genera with species which occur in both realms. The graphs clearly show a steep decline in genera confined to bathyal palaeodepths. The increase in genera confined to the abyss is small while the number and percentage of genera represented in both realms, particularly since the Pliocene is notable.

In order to determine whether certain elements were more involved than others in this invasion of the abyss, the fauna has been divided into 6 groups. Although these groupings are somewhat arbitrary, it is thought preferable to a division into families, for example, which exercise would have involved too many categories to maintain clarity and cohesion. The 6 groups are:

- | | |
|--|-------------|
| 1 Bairdiacea and Cypridacea | (15 genera) |
| 2 <i>Krithe</i> and <i>Parakrithe</i> | |
| 3. Bythocytheridae | (13 genera) |
| 4. <i>Eucythere</i> , <i>Cytheropteron</i> , <i>Aversovalva</i> and <i>Eucytherura</i> | |
| 5. Trachyleberididae | (34 genera) |
| 6. Other genera | (23 genera) |

The genera in Table 2 are arranged according to these 6 groups and Fig. 5 illustrates the Miocene to Quaternary numerical and percentage distribution of the species and the percentage distribution of the genera of each group. Although each group illustrates a decline in species diversity from Miocene to Pliocene, which in groups 1 and 4 is steep, all exhibit enhanced diversities in the Quaternary. This diversity increase is notable in all cases but particularly so with respect to group 1. The percentage of species of each group in the total fauna, however, shows an overall decrease in groups 2 and 4, and an overall increase in groups 1, 3 and 6. Both groups 2 and 5 enjoyed a higher percentage importance in the Pliocene than earlier or later.

With respect to genera, groups 1, 5 and 3 exhibit an overall percentage decline, while groups 6 and 4 illustrate an increase.

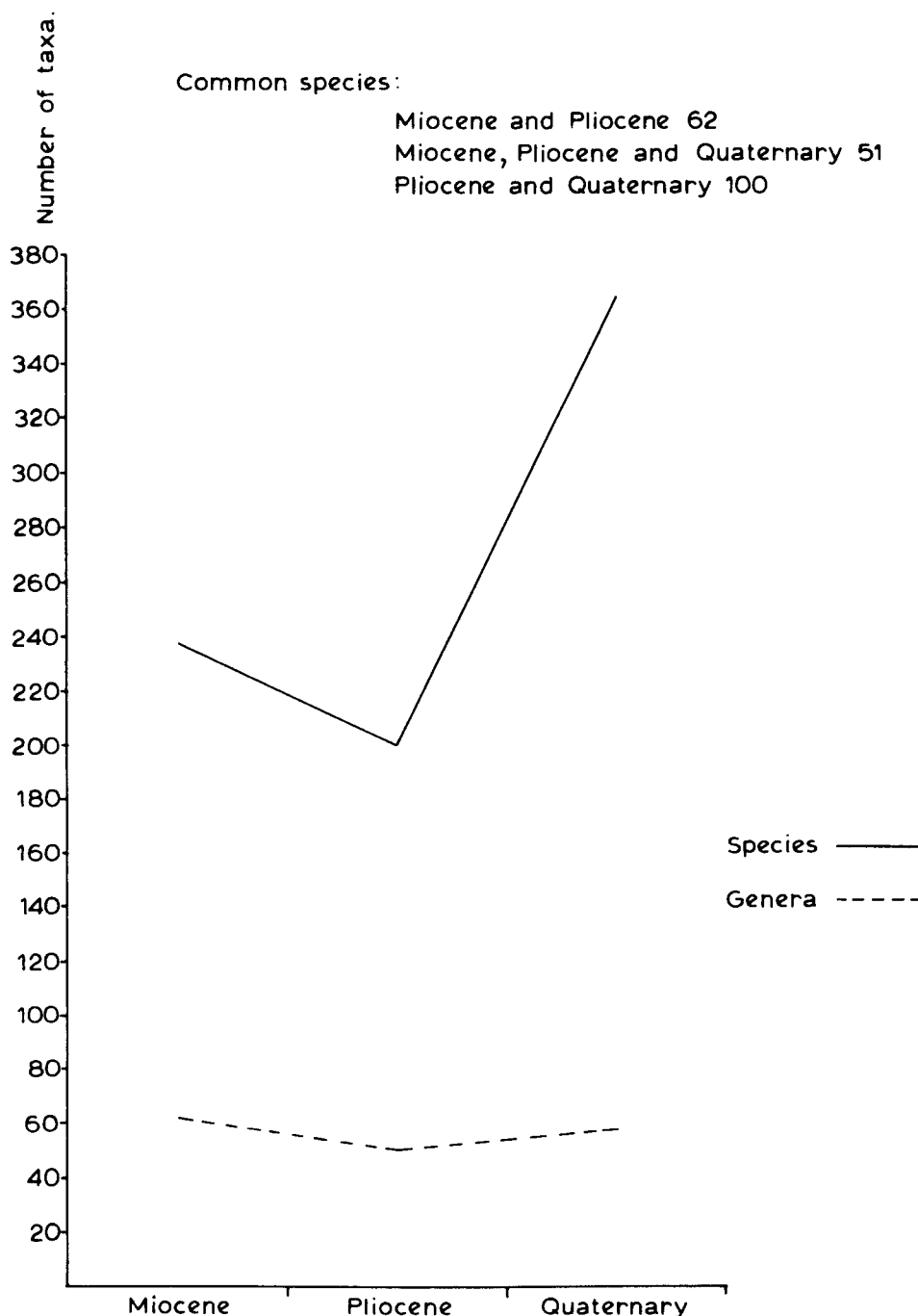
The various phenomena exhibited in Fig. 5 will be largely explained in the discussion of Figs. 6–8. In these figures the species and genera of each group are considered with reference to their palaeodepth distribution

through the Miocene to Quaternary interval.

Fig. 6 plots graphically the numerical distribution of the species of each group according to whether they are confined to bathyal or to abyssal palaeodepths or whether they occur in both realms. Fig. 7 plots the three categories of species of each group as percentages of the total fauna of each group in each system.

Group 1, although illustrating an overall increase in the number of bathyal only species shows a clear decline, from the Pliocene, in their percentage of the total group 1 fauna. Abyssal only species in this group decline from the Miocene to the Pliocene but increase steeply in the Quaternary where numerically and by percentage they exactly equal the bathyal only species. Species occurring

Fig.2. Total number of genera and species, Miocene to Quaternary and number of common species.



in both realms also increase overall. Although the main features illustrated by the group as a whole can be

demonstrated by a number of genera, perhaps the best example is *Argilloecia* (Table 2). In the Miocene this

Fig.3. Number and % of species confined to bathyal and to abyssal depths and of those which are both bathyal and abyssal.

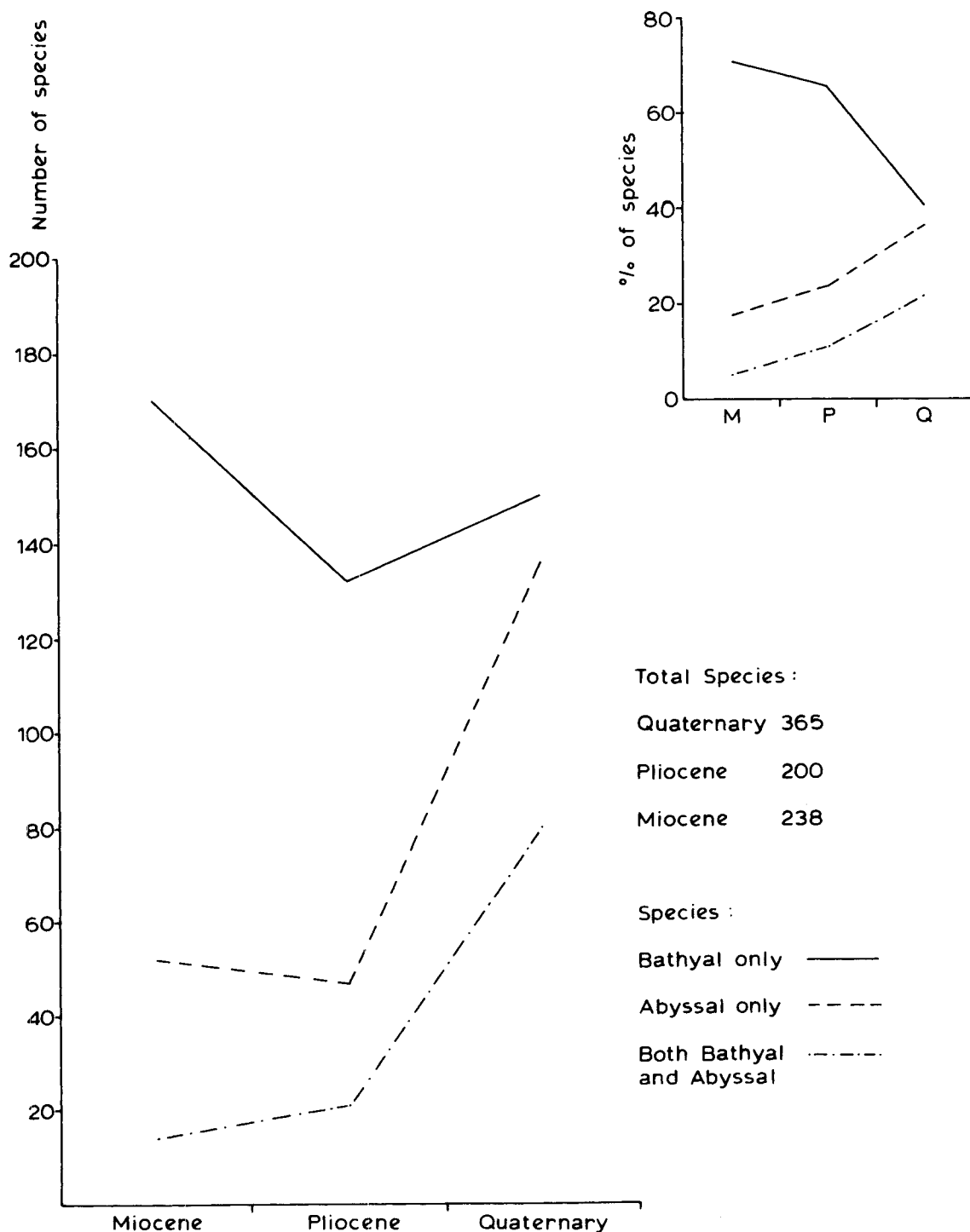
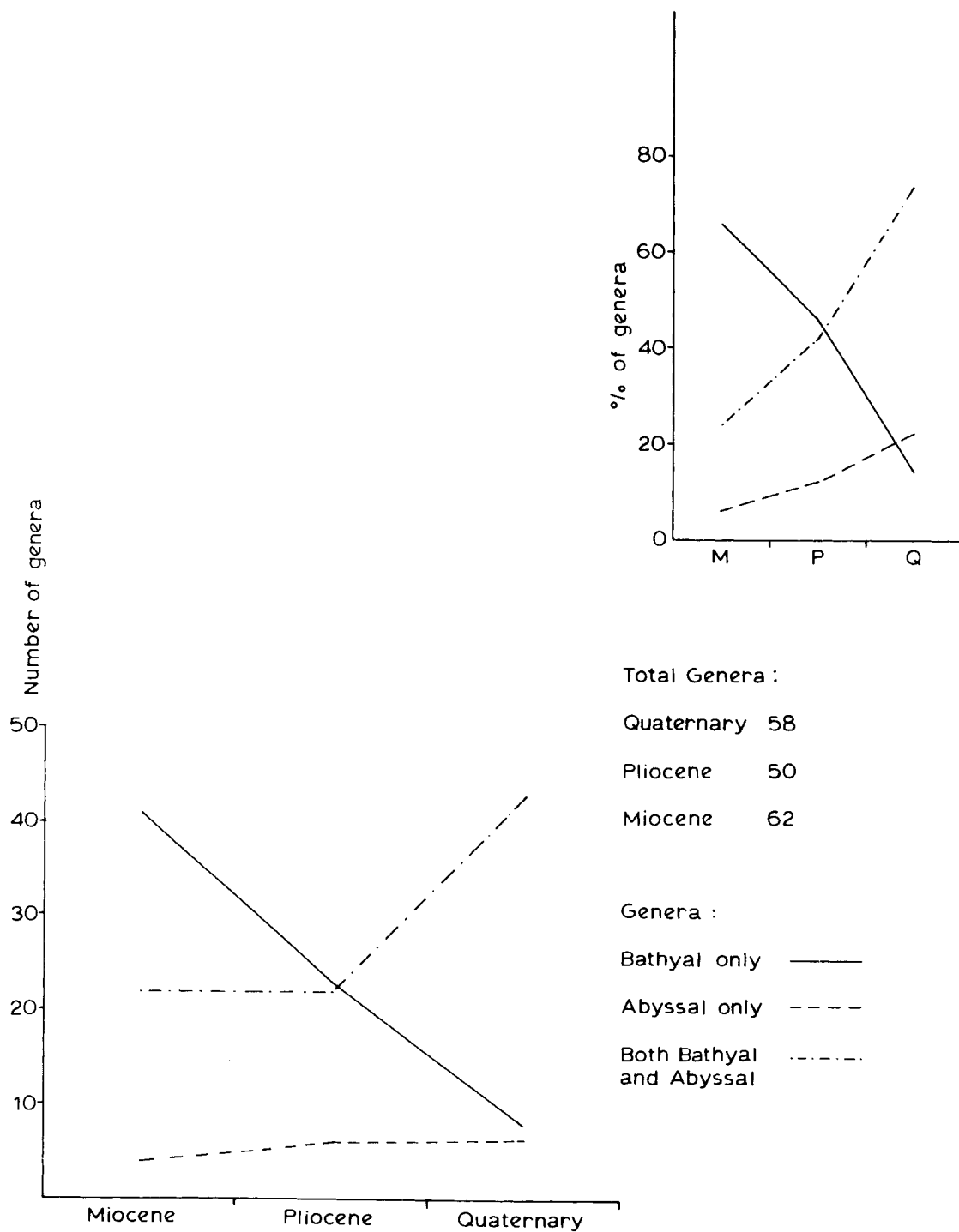


Fig.4. Number and % of genera confined to bathyal and to abyssal depths and of those which are both bathyal and abyssal.



genus is represented by 17 species of which 11 (64.7%) are bathyal only, 5 (29.4%) are abyssal only and just 1 (5.9%) occurs in both realms. In the Pliocene there is a decline to 11 species of which 9 (81.8%) are bathyal only, none are abyssal only and 2 (18.2%) occur in both realms. The number of species almost doubles into the Quaternary with 21 of which 9 (42.9%) are bathyal only 7 (33.3%) are abyssal only and 5 (23.8%) occupy both realms.

Argilloecia and the species of the group as a whole clearly show the progressive invasion of the abyss. From Table 2 other genera can be selected, such as *Neonesidea*, *Bairdoppilata*, *Bythocypris*, *Zabythocypris*, *Propontocypris*, *Australoecia* and *Paracypris* which in varying degrees illustrate the same phenomenon.

In group 2, both *Krithe* and *Parakrithe* are thought to have been early invaders of the deep sea and this is largely confirmed by Table 2 and Figs. 6 and 7. It is interesting to note that no pre-Quaternary species of these genera are known to occur in both realms. In the Quaternary, while no *Parakrithe* species are both bathyal and abyssal, a large number (15) and percentage (28%) of *Krithe* species are encountered in both realms for the first time.

Krithe seems better adapted to deep sea environments than any other ostracod genus and the author's experience is that it is similarly highly diverse in all the world's oceans from the late Palaeogene onwards. This high diversity has been masked by the taxonomic "lumping" of species of the genus by previous authors, such as Peypouquet (1975, 1977, 1975) who regard most *Krithe* species as being capable of contemporaneously existing as distinct ecomorphotypes at different depths and which exhibit as much as 200% size (length) difference between them. In a subsequent paper it is intended to present a more realistic taxonomic treatment of the genus.

All species of the Bythocytheridae (group 3) are bathyal only in the Miocene and Pliocene. While the number of such species, after declining in the Pliocene, remains constant overall, the number of abyssal only species in the Quaternary which first appear at that time, exceeds the former. Only one species of this group, in the Quaternary, occurs at both bathyal and abyssal palaeodepths.

Table 2 shows that 5 bythocytherid genera are confined (in this study) to the Miocene; that 3 genera occur for the first time in the Pliocene and a further 4 in the Quaternary. *Bythocythere* probably illustrates the invasion of the deep sea best; *Bythoceratina* rather less convincingly. *Pseudocythere* appears for the first time in deep water in the Quaternary with $\frac{2}{3}$ of its species confined to the abyss.

The four genera of group 4 collectively illustrate a small decline in numbers of bathyal only genera (Fig. 6) but a steep decline in their percentage (Fig. 7). The over-

all increase in abyssal only species and those occurring in both realms is also well demonstrated in both Figs. 6 and 7.

Cytheropteron and *Aversovalva* (Table 2) particularly clearly illustrate the invasion of the abyss. *Cytheropteron* is represented in the Miocene by 30 species of which 22 (73.3%) are bathyal only, 6 (20%) abyssal only and just 2 (6.6%) occur in both realms. In the Pliocene a similar depth distribution obtains with, of the 31 species, 26 (83.9%) being bathyal only, (9.7% abyssal only and again 2 (6.4%) being found in both realms. There are 57 Quaternary species of which 23 (40.3%) are bathyal only and a similar number 22 (38.6%) are abyssal only. Twelve species (21.1%) occur at both bathyal and abyssal palaeodepths. *Aversovalva* follows a very similar trend.

The Trachyleberididae (group 5) exhibit a steep decline in the number of bathyal only species from Miocene to Pliocene with a partial recovery into the Quaternary. This is matched by their percentage. Abyssal only species increase to the Pliocene, then maintain their numbers although their percentage declines. The most notable feature of this group is the regular steep increase, in the Miocene to Quaternary interval of species which are both bathyal and abyssal in their distribution. The progressive invasion of the abyss is best shown in *Bradleya* and *Poseidonamicus* (Table 2, Whatley *et al.*, in press a, b, c).

Although a very heterogeneous mixture of genera, the species of group 6 also clearly demonstrate the increase in the number and percentage of abyssal only species at the expense of the bathyal only species. Species of this group found in both realms remain low throughout the interval studied.

Fig. 8 largely confirms what earlier figures have demonstrated with respect to the abyssal invasion, in this case by illustrating the percentage of genera which are bathyal only, abyssal only, or which occur in both realms.

While all genera in groups 2 and 4 belong to the latter category, each of the other groups shows a steep overall decline in the percentage of bathyal only genera with a concomitant increase in the percentages of abyssal only genera (groups 3 and 6) and genera with species occurring in both environments (groups 1, 3, 5, 6).

The evidence given above clearly indicates that a distinct ecological shift took place among deep sea Ostracoda in this region from the Miocene to the Quaternary. This resulted in enhanced abyssal specific diversities by the Quaternary, an absolute and proportional decrease in bathyal diversity and a notable increase in those species able to exist in both bathyal and abyssal palaeodepths. This evidence is based on data obtained from all 18 DSDP sites plus the samples from the Loyalty Basin, not all of which have strata of each of the ages concerned, or have been studied for only parts of the stratigraphical column.

Fig. 5. Number and % of species and % of genera in each of 6 groups of Ostracoda, Miocene-Quaternary.

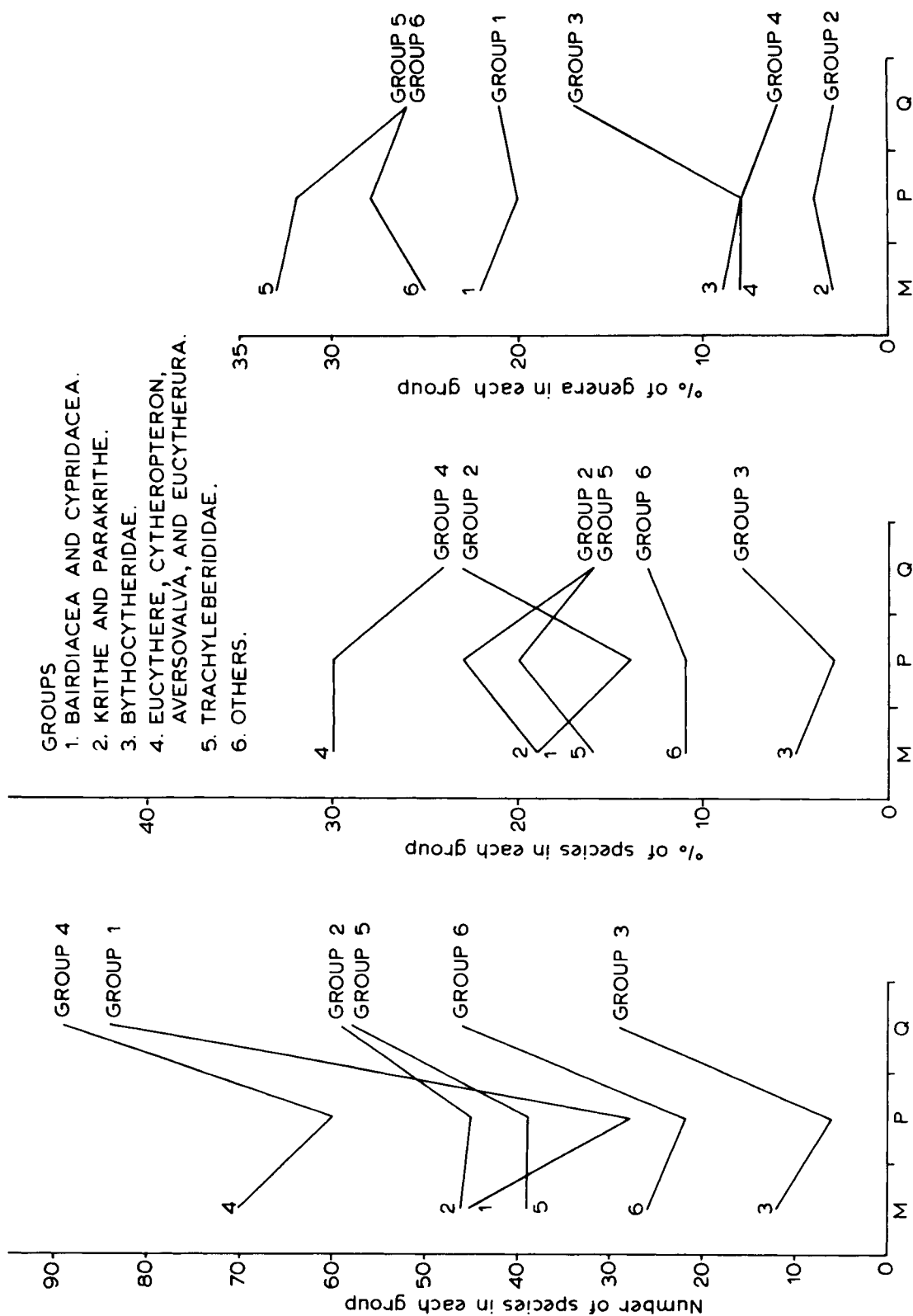


Fig.6. Number of species either bathyal, abyssal or both in each group, Miocene - Quaternary.

Key as in Fig. 4.

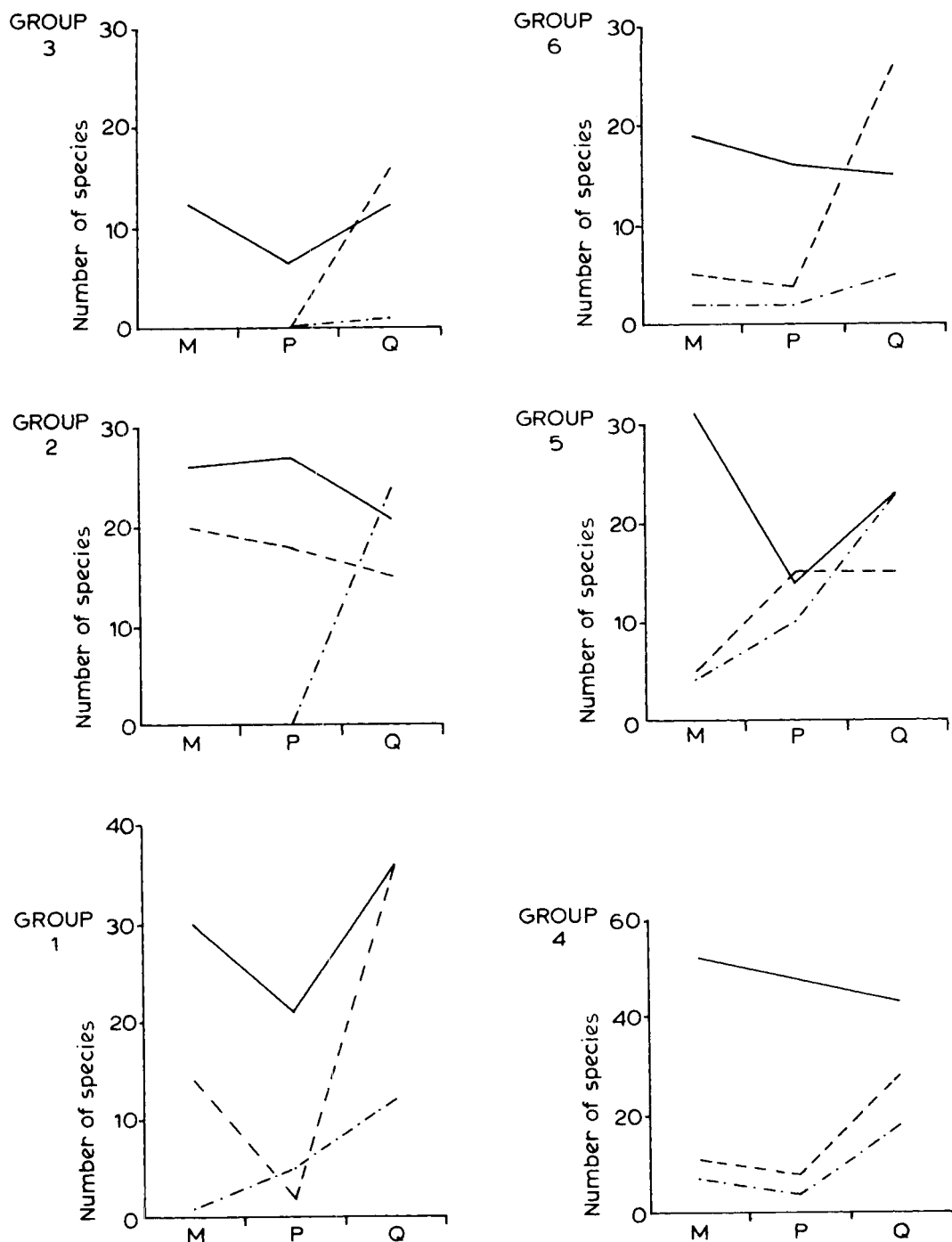


Fig.7. % of species, either bathyal, abyssal or both in each group.

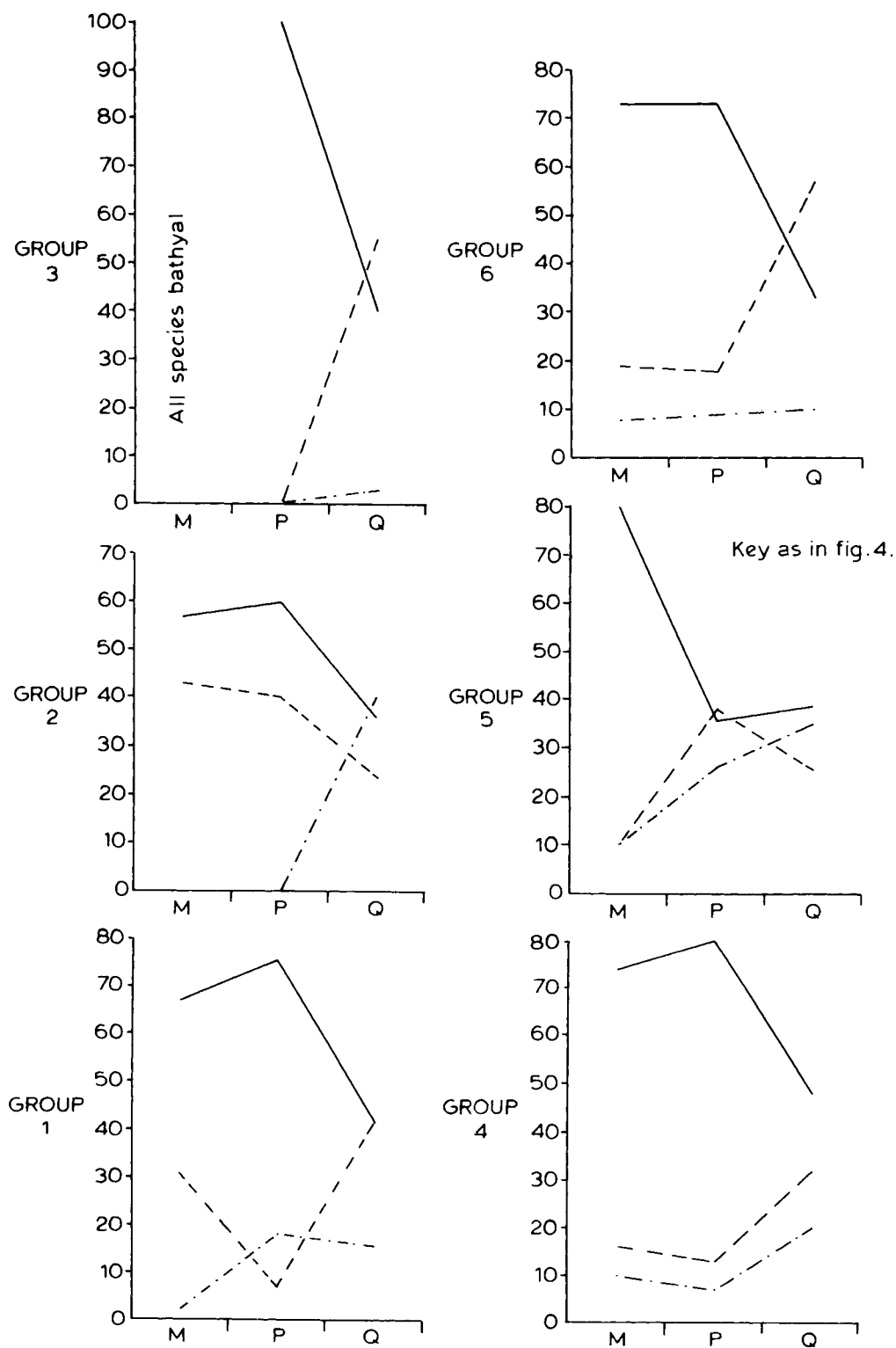


Fig.8. % of genera either bathyal, abyssal or both in each group, Miocene - Quaternary.

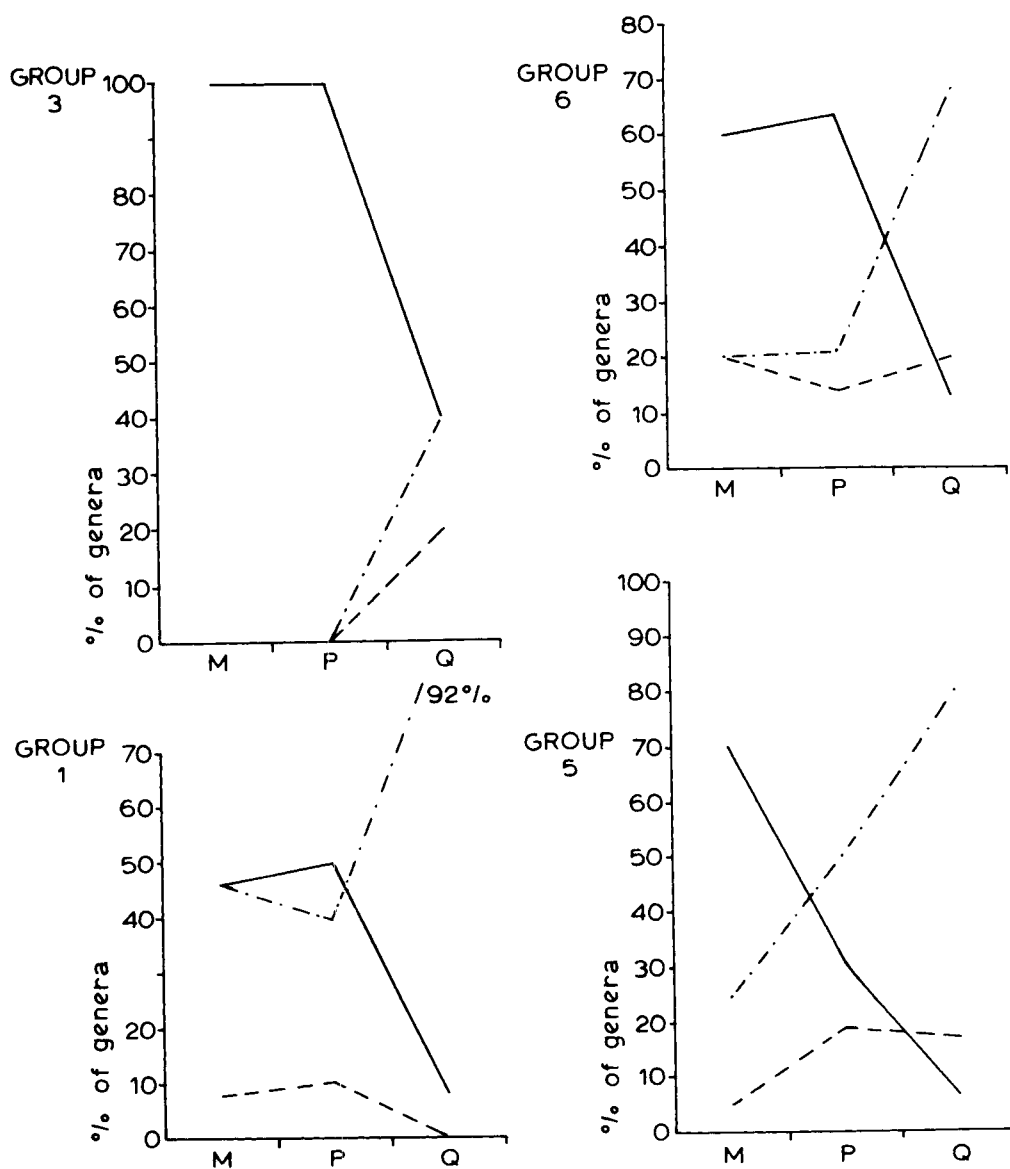
GROUP 4. All genera both Bathyal and Abyssal, Miocene - Quaternary

Bathyal only ———

Abyssal only - - - -

GROUP 2. All genera both Bathyal and Abyssal, Miocene - Quaternary

Both Bathyal and Abyssal - · - · -



AN ANALYSIS OF THE FAUNAS OF FIVE SITES; MIOCENE TO QUATERNARY

The faunas of 5 sites have been studied continuously and comprehensively from the Miocene to the Quaternary. These are Site 209, on the outer edge of the Queensland Plateau, Sites 207 and 208 on the Lord Howe Rise (these three sites were all at bathyal palaeodepths during the Neogene and Quaternary, ranging between some 1300 m and 1500 m) and Sites 64 and 289, which straddle the equator (these were at abyssal palaeodepths during this interval; some 2000 m to 2200 m). Fig. 9 provides numerical data on the species from each of the 5 sites. The total number of species at each site clearly shows that diversity throughout the Neogene and Quaternary was highest at the bathyal sites. Site 64 shows a steep increase in the number of species at that site and Site 289 also shows an increase, although the highest number occurs in the Pliocene. Fig. 9 also illustrates that the number of species common to more than 2 sites is very much reduced. However, in general, there is an increase in the common species between sites with time. Very important is the histogram illustrating the more than threefold increase in the number of species occurring contemporaneously at both bathyal and abyssal palaeodepths from Miocene to Quaternary.

Figs. 10, 11 and 12 plot the number of species common between the 5 sites for the Miocene, Pliocene and Quaternary respectively. The sites are arranged in a very approximate geographical order. With respect to Fig. 10 it is important to note:

1. The relatively low number of species in the abyss compared to the bathyal.
2. The very few species common between bathyal and abyssal sites.
3. The low number of species common to Sites 64 and 289.
4. The rather low number of species common to Sites 207 and 208 and to Sites 208 and 209.
5. The high number of species common to Sites 207 and 209. Although these two sites, on the southern part of the Lord Howe Rise and Queensland Plateau respectively are today separated by abyssal palaeodepths, this intervening area probably only subsided to these depths in the late Palaeogene or earliest Neogene. The high correlation between these two sites is interpreted as reflecting their common origin on an originally integral area of shelf which subsequently subsided to bathyal depths before being divided into two by the central part subsiding still further to abyssal depths. This suggestion does not however, explain the lower correlation between the other bathyal sites in the Miocene.

Fig. 11 illustrates the following:

1. A small but significant increase in the number of species in the abyss.

2. A significant increase in the number of species common to bathyal and abyssal sites.
3. A 40% increase in the number of species common to Sites 64 and 289.
4. A major increase in the number of species common to Sites 207 and 208 and a marked increase in the number of species common to Sites 208 and 209.
5. A small but significant decrease in the number of species common to Sites 207 and 209.

Fig. 12 completes this history by demonstrating:

1. The presence of many more species in the abyss.
2. A considerably enhanced number of species common to bathyal and abyssal sites.
3. An increase in the number of species at Site 64 although the number at Site 289 has declined since the Pliocene.
4. A slight decrease in the number of species common to Sites 207 and 208 and to Sites 208 and 209.
5. A sustained decline in the number of species common to Sites 207 and 209 which is interpreted as the increasing effect of abyssal separation of the two sites.

This history of events depicted at these 5 sites in the Miocene to Quaternary interval mirrors those discussed earlier with respect to all the sites and illustrated in Figs. 3–8. It provides further evidence for the progressive invasion of the abyss, for a proportional decline in the importance of bathyal only species and for an increase in the number of species able to live at both bathyal and abyssal palaeodepths.

The breakdown of isolation during the Neogene seems also to have occurred on the only guyot we have studied. Although we have only studied Miocene and Pliocene samples on the Ita Mai Tai guyot (Site 200), Fig. 13 illustrates in the species and genera which occur there, both in terms of total numbers and in terms of those taxa which (in this study) are exclusively found there, a steep decline from the Miocene to the Pliocene.

CONCLUSIONS

The following conclusions can be drawn from this study:

1. Neogene and Quaternary bathyal and abyssal faunas in the S.W. Pacific exhibit a much higher generic and specific diversity than previous studies would suggest. From my own observations this can certainly be applied to most and probably to all of the world's oceans.
2. In the areas studied, there is a decline in both specific and generic diversity from the Miocene to the Pliocene, followed by an increase, very marked for species, to the Quaternary. While the high diversity of the Quaternary in this area is probably nearly matched in the N. Atlantic (personal observation), not enough evidence exists to substantiate the Pliocene decline elsewhere in the deep sea. Shelf faunas do not reflect this Pliocene decline which may be more apparent

Fig 9. Data on the numerical distribution of species from D.S.D.P sites 207, 208, 209, 64, 289, Miocene to Quaternary.

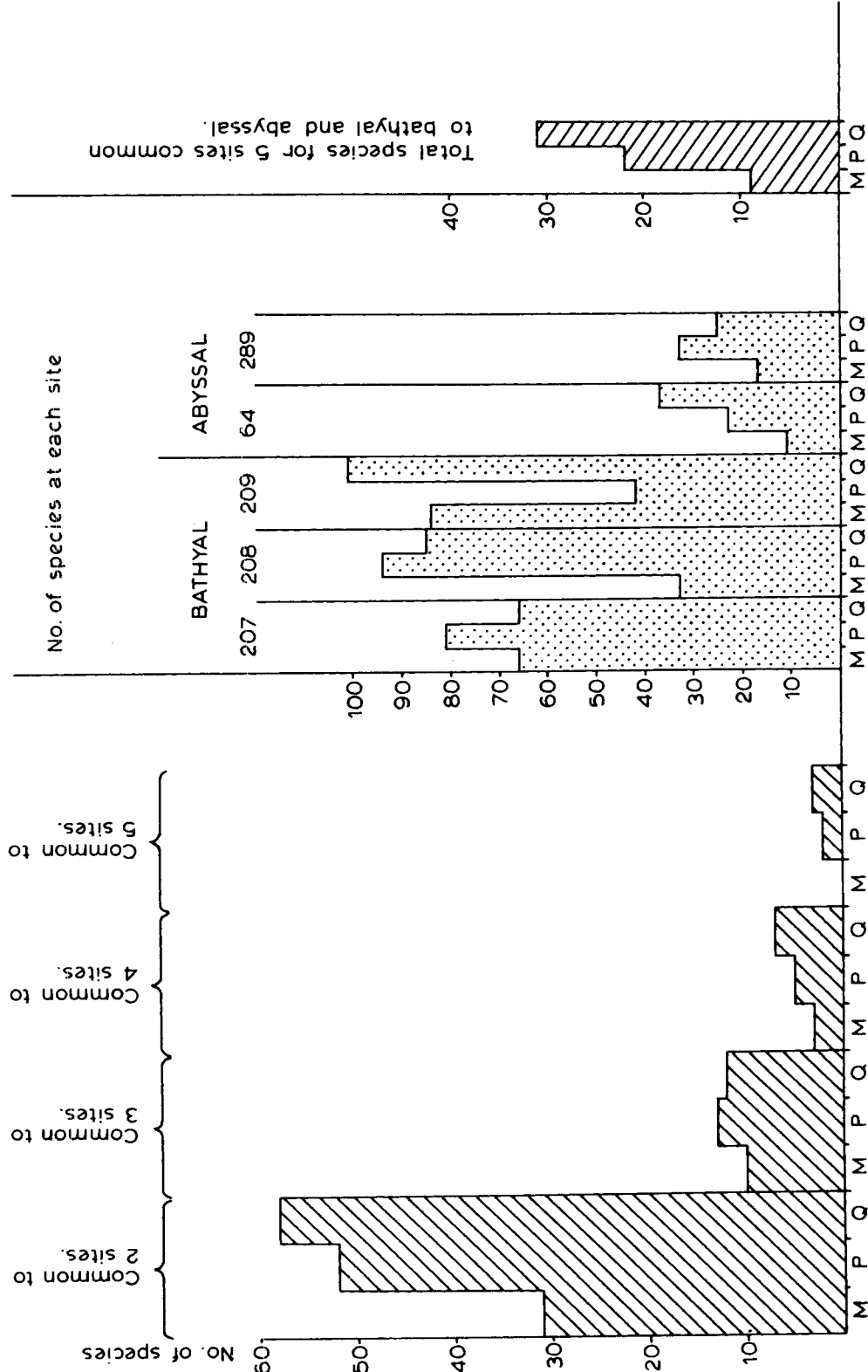
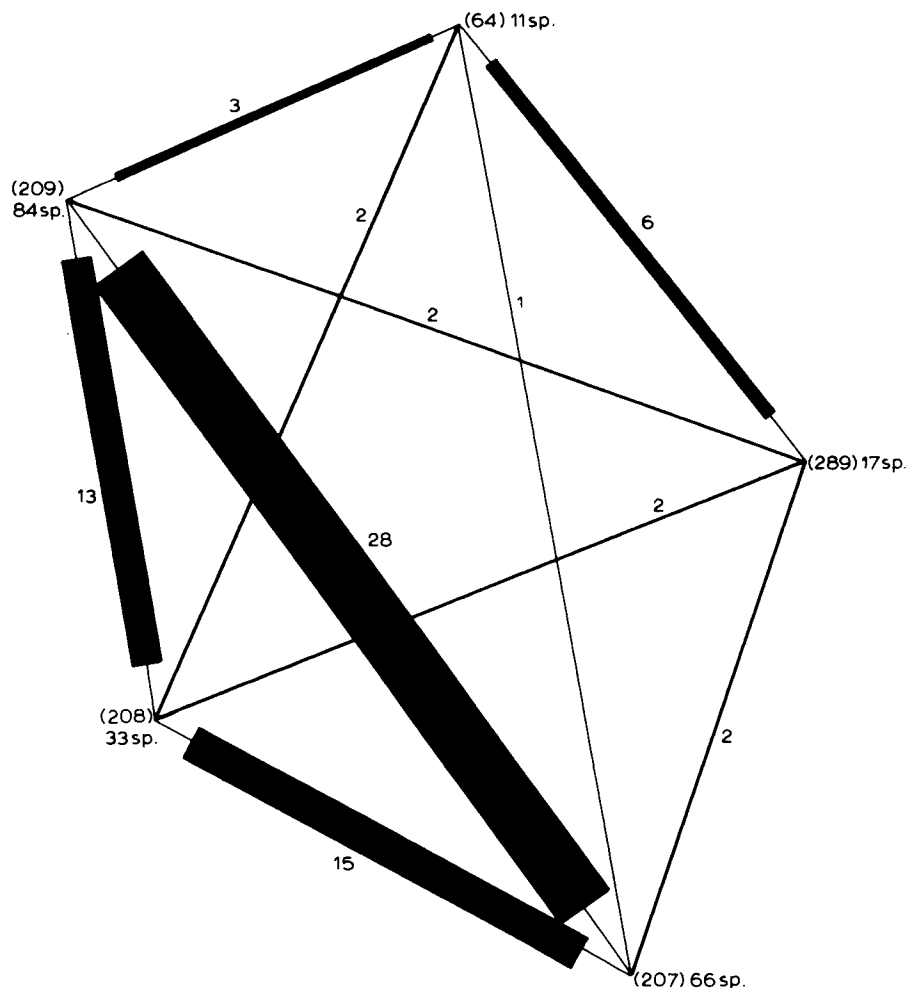


Fig.10. No. of common species between 5 sites

MIocene
 Sites 207, 208, 209 bathyal
 Sites 64, 289 abyssal



than real. That Miocene diversity is abnormally high is suggested by studies on *Bradleya* and *Poseidonamicus* (Whatley *et al.*, in press a, b, c).

3. A major downslope invasion of the abyss took place between the Miocene and Quaternary in the S.W. Pacific. Species confined to bathyal palaeodepths decline in numbers and percentage and those species confined to abyssal palaeodepths, together with those which occur in both environments, increase substantially. Although insufficient evidence exists to prove that this phenomenon is a universal one, personal knowledge of Indian and Atlantic Neogene and Quaternary faunas suggests that this is possibly so. The causes of this invasion are not certain. It may be associated with major palaeoceanographic or

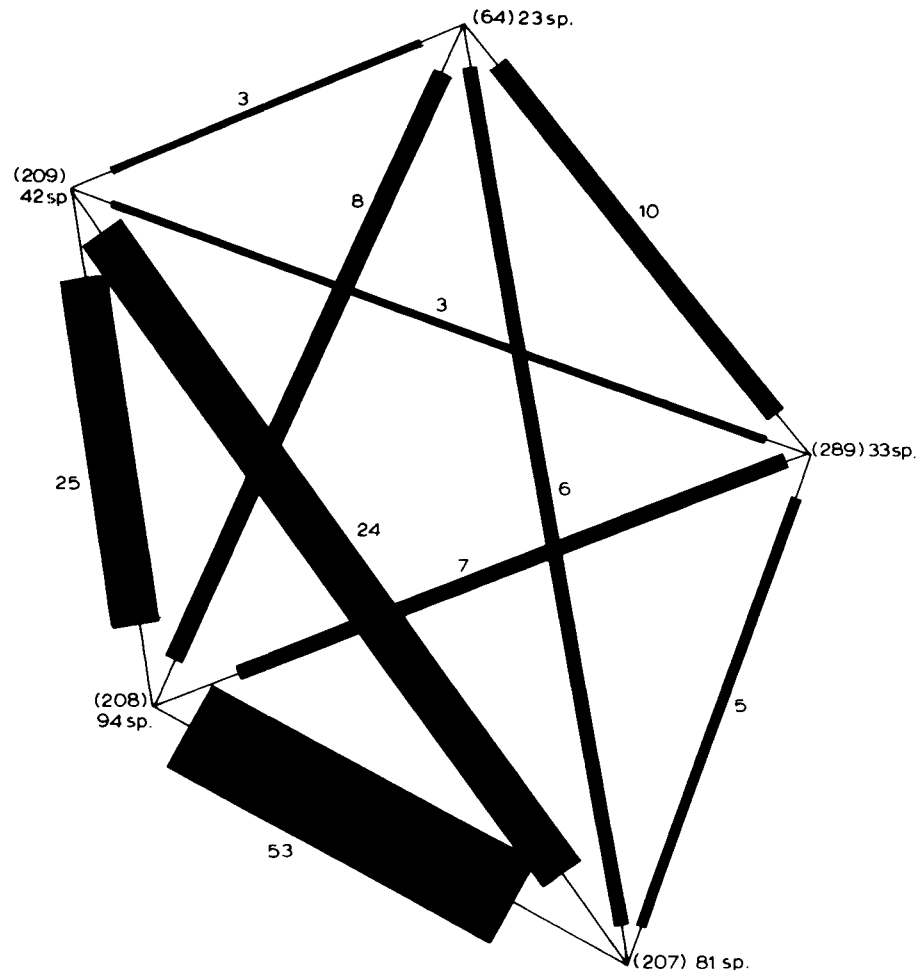
palaeoclimatic events or it may be the culmination of a process long in existence. It is hoped that our studies on the Palaeogene will help to resolve this.

4. In general, each of the 6 groups into which the fauna has been divided, exhibit the phenomena outlined in 1–3 above.
5. A study of 5 sites, continuously studied from the Miocene to the Quaternary, confirms the conclusions drawn in 1–3 above which were made on the basis of a study of all 18 sites.
6. The fauna isolated at bathyal depths on the Ita Mai Tai guyot surrounded by an extensive and very deep abyssal plain, diminished in both numbers and its degree of endemism from the Miocene to the Pliocene.

Fig.11. No. of common species between 5 sites

PLIOCENE

Sites 207, 208, 209 bathyal
Sites 64, 289 abyssal



Any conclusions drawn from this study cannot, for the moment, be proved to be applicable to other areas. Also, since it is believed that in this area there exists, between Australia and New Zealand, an important locus of involuntary tectonically controlled induction into the deep sea, it is possible that the results obtained for the S.W. Pacific may be atypical. Notwithstanding these qualifications, however, as yet unpublished and incomplete, studies on the northern Indian Ocean and North Atlantic do suggest that certain aspects of the conclusions which can be drawn from this study of the S.W. Pacific Neogene and Tertiary may be more generally applicable. This seems particularly likely with respect to the largely post-Miocene invasion of the abyss.

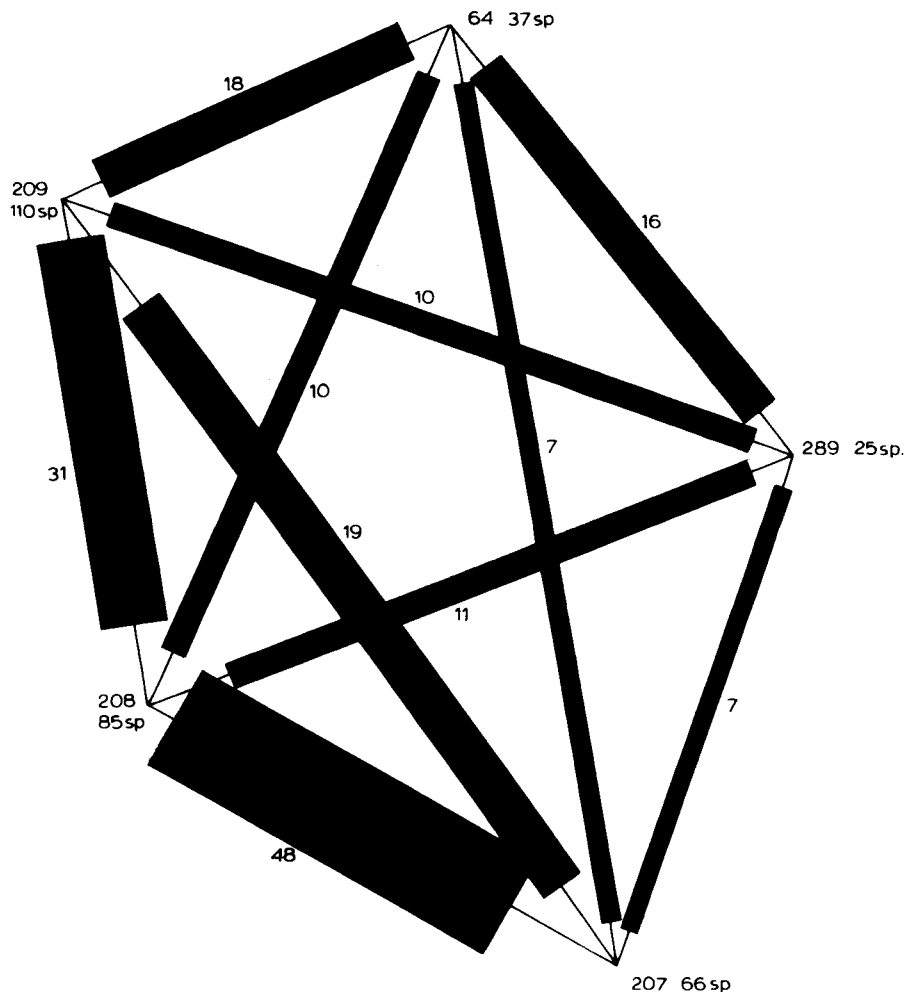
Continuing research in the Palaeogene of the S.W. Pacific and in the Neogene and Quaternary of the North Atlantic will, it is hoped, resolve these matters one way or the other in the future and allow consideration of the causes of this migration.

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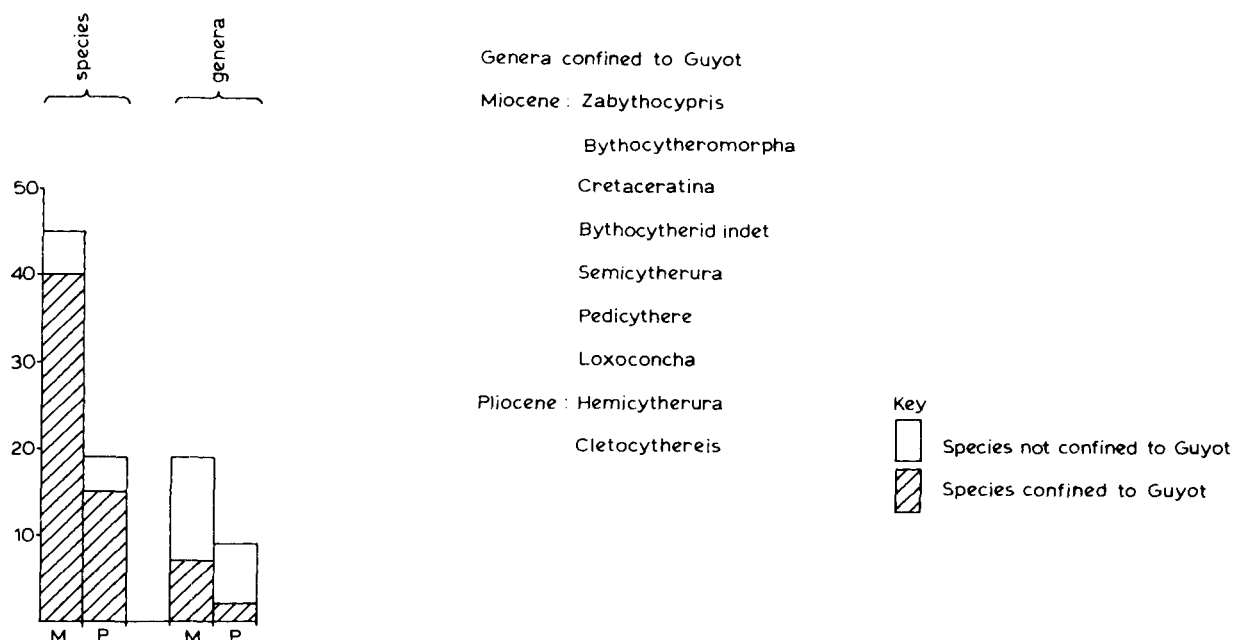
Fig.12. No of common species between 5 sites. QUATERNARY
Sites 207, 208, 209 bathyal
Sites 64, 289 abyssal



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Fig.13. Total number and number of species and genera confined to the Ita Mai Tai Guyot, D.S.D.P. 200 (Not sampled in Quaternary)



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