ASPECTS OF THE EVOLUTION OF CAINOZOIC DEEP-SEA OSTRACODA IN THE SOUTHWEST PACIFIC

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ABSTRACT

The simple species diversity (both recorded and cumulative) of deep sea Ostracoda throughout the Cainozoic of the Southwest Pacific is shown to fluctuate considerably as does the level of originations and extinctions of species. The former exceed the latter throughout the Palaeocene and Eocene thus allowing diversity to build up to its acme in the middle Eocene where, in NP Zone 16 extinctions exceed originations for the first time. These events, the subsequent late Eocene/early Oligocene diversity crash followed by a recovery into the late Oligocene, and the diversity and evolutionary high low points of the Neogene and Quaternary, are discussed with reference to contemporary oceanic events and compared to circumstances in other oceans.

Key words: Ostracoda, Deep-sea, Cainozoic, Middle Eocene, Evolution, Southwest Pacific.

RESUMEN

ASPECTOS DE LA EVOLUCION DE LOS OSTRACODOS CENOZOICOS DE MAR PROFUNDO EN EL PACIFICO SUR-OCCIDENTAL. La diversidad específica (tanto registrada como acumulativa) de los ostrácodos de mar profundo en el Pacífico sur-occidental, ha fluctuado considerablemente durante el Cenozoico, en igual forma que el nivel del aparecimiento y extinción de las especies. Las primeras exceden a las últimas a través del Paleoceno y del Eoceno, permitiendo que la diversificación alcance su apogeo en el Eoceno medio, donde se produce la extinción de 16 especies en la zona NP16, excediendo, por primera vez, a los aparecimientos. En el presente trabajo se analizan estos sucesos, como también la caída de la diversidad durante el Eoceno tardío/Oligoceno temprano seguido por una recuperación durante el Oligoceno tardío, y una escasa diversificación y evolución durante el Neógeno y el Cuaternario, refiriéndolos a los sucesos oceánicos contemporáneos y comparándolos con los parámetros de otros océanos.

Palabras claves: Ostrácoda, Mar profundo, Cenozoico, Eoceno medio, Evolución, Pacífico sur-occidental.

INTRODUCTION

Major changes are known to have taken place in the specific diversity and in the rate of evolutionary turnover, as measured by levels of extinctions and originations, of deep-sea Ostracoda throughout the Cainozoic. This has been demonstrated by Benson, 1990; Benson *et al.*, 1985; Coles, 1990; Coles *et al.*, 1990; Whatley, 1983; Whatley and Coles, 1991; Whatley *et al.*, 1983; Steineck *et al.*, 1988.

In most cases, changes in diversity and/or evolutionary rates have been considered as responses to environmental perturbations brought about by local, regional or global changes. For example, around and about 38-40 Ma, the World Ocean, which since the Permian (260 Ma) has been single layered and thermospheric, entirely changed its character and became, in a relatively short time, two layered. This involved the creation of a deep, cold psychrospheric layer, separated by a pronounced thermocline from a shallow, warm, thermospheric layer. This dual layered ocean could not have come about during the Mesozoic because of the absence, during the entire duration of that interval, of polar ice.

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However, due to progressive global cooling during the early Palaeogene, ice accumulated at the poles, especially in the Antarctic. The dense, cold and very saline waters generated in these high latitudes sunk to the ocean bottom and gradually occupied the entire abyssal and deeper bathyal realms of all the world's ocean basins.

In certain regions, notably in the western Pacific, the arrival of this very corrosive water mass is marked by a major unconformity, which in places marks the removal of considerable deposits of Eocene, Palaeocene, and in places Cretaceous sediments (Edwards, 1975; Kennett *et al.*, 1972, 1974; Kennett, 1980.

The change, from a single layered ocean in which temperatures even in the greatest depths probably were not less than 10°C, to one in which the same depths would see temperatures in the range 0°-2°C, was the most drastic that took place in the Cainozoic. Without question it imposed a major challenge to the pre-existing benthos to adapt to the new conditions and also to new immigrants who would encounter environmental thresholds, biological, physical and chemical, quite beyond their prior experience.

The inception of the thermocline also imposed a major barrier to migration, not only in terms of the vertical movement of planktonic animals (Angel, 1968) but also between benthonic animals living on either side of it. In most cases these communities have, particularly in high latitudes, remained cut off from one another because of the difficulty they would experience in attempting to cross a temperature threshold of 10°C or more in a few metres. Although some planktonic and nektonic animals regularly migrate through this boundary, very few members of the benthos are capable of achieving this.

In high latitudes the thermocline is a less potent barrier and relatively easy isothermal pathways exist for migration to and from the deep sea for animals of all modes of life.

Benson (1990) summarizes many of his earlier statements concerning the effect on the ostracod fauna in the formation of the psychrosphere. The present author (Whatley *et al.*, 1983), Whatley and Coles (1991) and his students (Coles, 1990, 1989; Millson, 1991) have not, in the areas they have studied, encountered such marked faunal changes as those noted by Benson.They have, however, as will be shown below, encountered considerable faunal changes at somewhat different times during the Tertiary.

Global climatic changes subsequent to 38-40 Ma had major consequences for terrestrial biotas and for those living in shallow seas or in the upper parts of the oceanic water column. On the whole, however, the deep sea benthos, being encapsulated by thousands of metres of water from the more direct effects of these changes, exhibit either a weaker response or none at all. As will be seen below, however, some major diversity and extinction/origination rate changes subsequent to 38-40 Ma may be attributed to climatic change, particularly in the Pliocene and Quaternary.

Other major events, which had consequences of varying intensity for deep sea faunas during the later Cainozoic (this being largely dependant upon geographical proximity in many cases) were mainly associated with tectonism. These include the closure of both the Iberian/North African and Asian ends of the Tethys in the Miocene, the closure of the Straits of Panama in the Pliocene and the opening of the Drake Passage.

Changes in the patterns of oceanic circulation, gyres, the widening of the North Atlantic and the development of the Arctic and Southern Oceans all took place during the Cainozoic, as did the major, largely Miocene orogeny which produced, among so many other mountain chains, those which rim the Pacific.

The Cainozoic began with the legacy of an extinction event at the Cretaceous/Tertiary boundary. Despite wild theories, invoking among other things extra-terrestrial agencies, an analysis of this event reveals its stepped nature and the author has already expressed his view that it may have been brought about by periodical yet sustained volcanic activity on a huge scale and has joined others in suggesting that the Upper Cretaceous history of eruption in the Deccan is a likely causal phenomenon (Whatley, 1990).

While the consequences of the end-Cretaceous extinction varies between different animal and plant groups, in Ostracoda considerable changes took place over the boundary in shallow water marine forms but in areas such as northern China, for example, very little change took place among non marine faunas, (Whatley, 1990a; 1990b). Benson (1990) estimates that only 15% of deep sea ostracod genera became extinct during this event. The preservation of the majority was probably due to the insulating effect of great depths of sea water. It must be emphasized, however, that the diversity of Upper Cretaceous deep sea Ostracoda was low; much lower than the levels which they were to achieve in parts of the Tertiary.

PALAEOGENE DEEP SEA FAUNAS IN THE PACIFIC

The only in depth study of these faunas is that of Millson (1988). Only parts of this doctoral dissertation have as yet been published and these are principally taxonomic in content (Whatley, 1983a,b; 1986; Whatley *et al.*, 1982, 1983, 1985, 1986). The publication of the remainder of this important study is in preparation. Benson (1990) provides diversity data on Palaeogene ostracods from the Indo-Pacific and Steineck *et al.* (1988) includes information on the Oligocene of the Central Pacific.

Millson (1988) studied 79 Palaeogene samples from 6 Deep Sea Drilling Project (DSDP) sites, the location of which are given in figure 1. Some details of each site are given in table 1 below:

The stratigraphical distribution of these samples and the number of species and genera they contain is given in table 2.

It is always difficult when studying Palaeocene faunas to be certain whether, if they are of low diversity, this is due to the immediate after effects of an extinction event at the Cretaceous/Tertiary boundary, or whether as may be the case in the present example, it is possibly the consequence of inadequate sampling.

Millson (1988) also examined Upper Cretaceous samples from 3 sites (289, 207, 208) but recorded ostracods only from the latter. It is interesting to note that of the 23 species recovered, less than half (11) became extinct at the Cretaceous-Terciary boundary. Four of the remainder did not survive the Palaeocene, 4 became extinct in the Eocene and 4 also occur in the Oligocene. Three of the latter are still present in the Duntroonian Stage of the upper Oligocene.

Many of the samples which Millson studied from sites 207, 208 and 277 were, in the Palaeocene and early Eocene, deposited at substantially shallower depths than obtained at those sites in the subsequent Palaeogene. Many of the ostracods recorded from the samples were of shelf species which, as subsidence at the sites took place, became at least locally extinct. Other species were able to adapt to the gradually and intermittently increasing depth and were thus involuntarily inducted into the deep sea (Whatley *et al.*, 1983; Millson, 1988). All these sites record a history of subsidence to depths of around 1300 to 1500 m by the Oligocene or early Miocene.

TABLE 1. LOCALITY, WATER DEPTH AND NUMBER OF SAMPLES STUDIED FROM 6 DSPD SITES IN THE SOUTHWEST PACIFIC

Site	Locality	Coordinates		PDWD	S
289	Ontong Java Plateau	158°30.69'E	00°29.92'S	2,206 m	4
209	Queensland Plateau	152°11.27'E	15°56.19'S	1,428 m	9
208	Lord Howe Rise	161°13.27'E	26°06.61'S	1,545 m	9
206	New Caledonia Basin	165°27.15'E	32°00.75'S	3,196 m	11
207	Lord Howe Rise	165°26.06'E	36°57.75'S	1,389 m	9
277	Campbell Plateau	166°11.48'E	52°13.43'S	1,214 m	26

S = number of samples

TABLE 2. STRATIGRAPHICAL AND DIVERSITY DATA FROM PALAEOGENE SITES IN THE SOUTHWEST PACIFIC

	Samples	Species	Genera
Oligocene	47	118	47
Eocene	34	202	70
Palaeocene	12	50	28

The simple species diversity of ostracods through the Palaeogene of the Southwest Pacific, based on the 6 sites and 68 samples listed in table 1, is shown

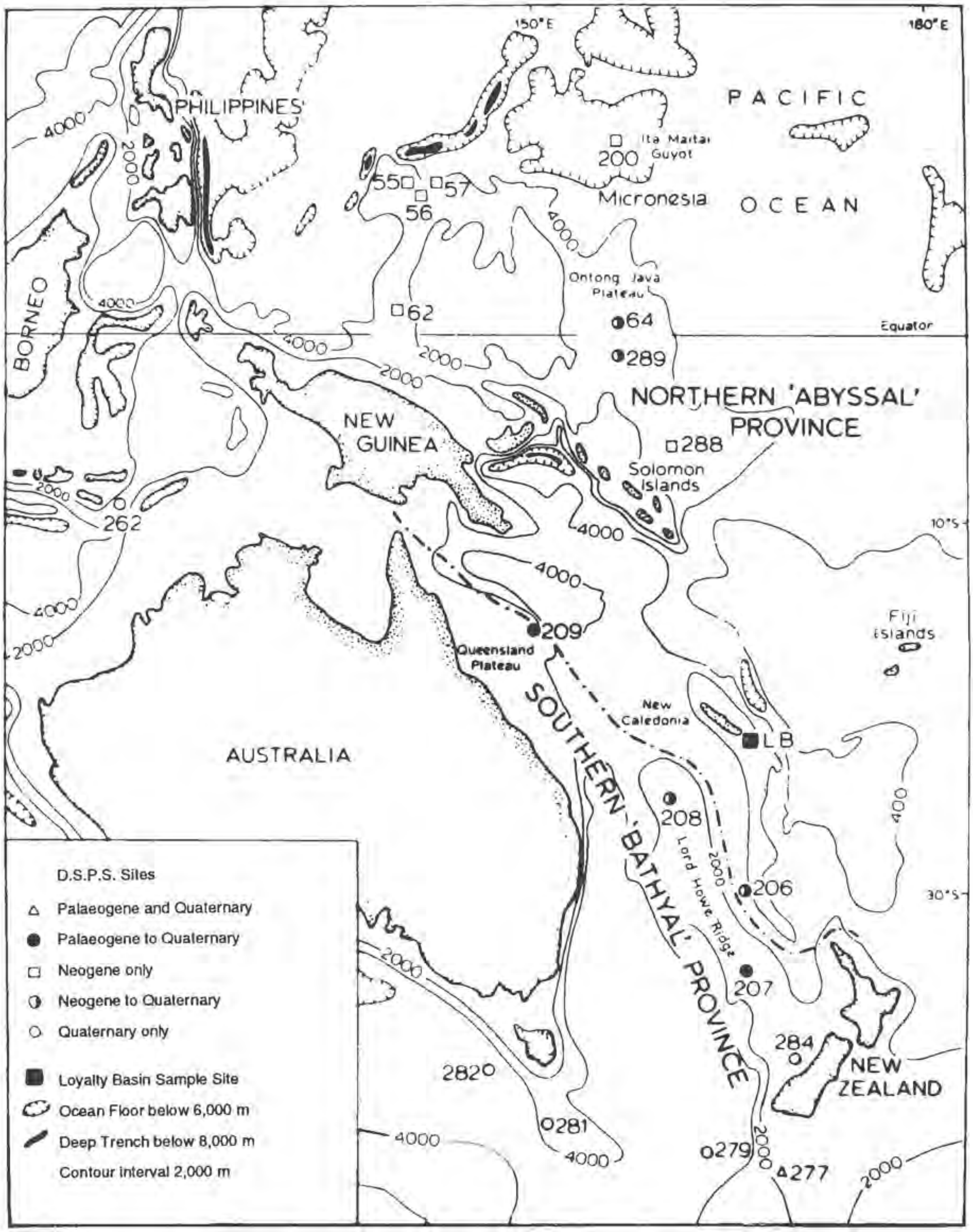

FIG. 1. Bathymetric and locality map of Deep Sea Drilling Project sites in the southwest Pacific.

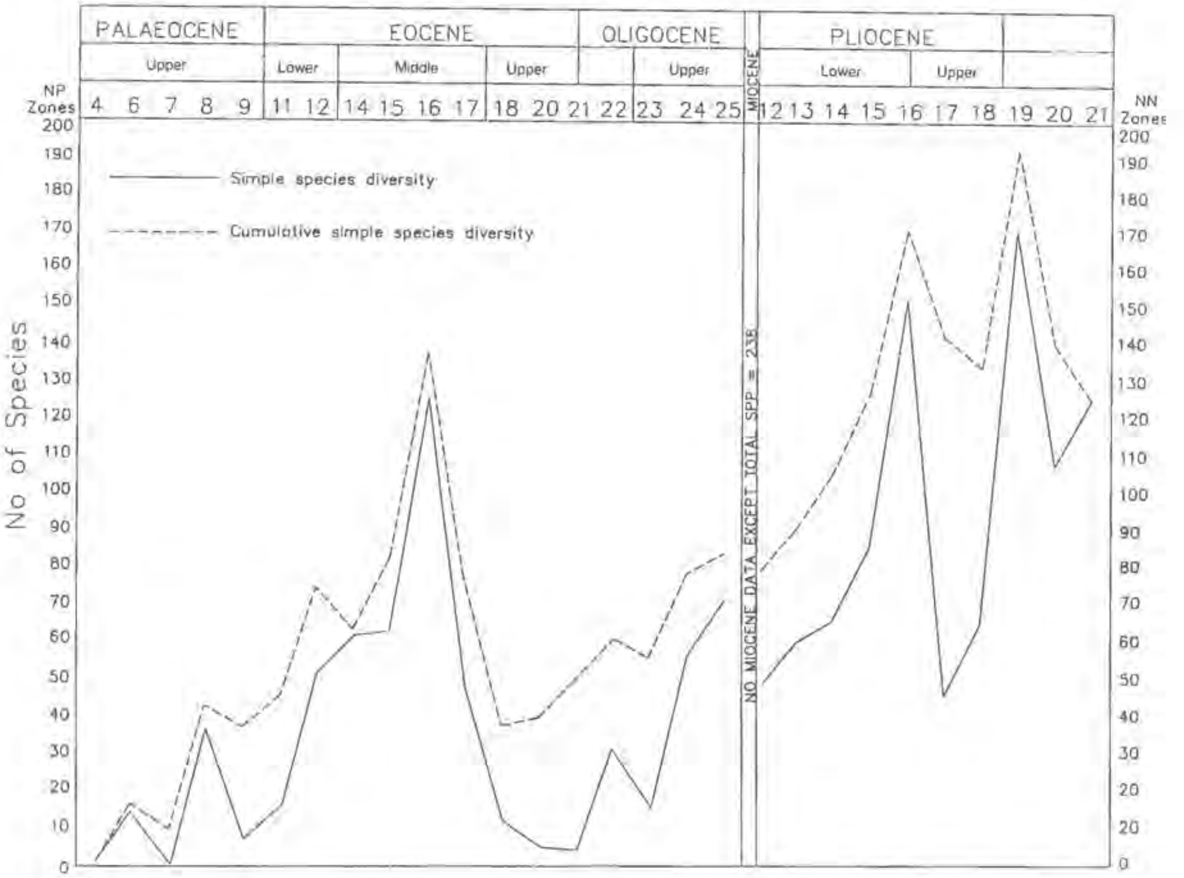

FIG. 2a. Simple species diversity and cumulative species diversity for the deep-sea Cainozoic of the Southwest Pacific.

in figure 2a. The solid line is drawn from actual occurrence by sample, while the dashed line records both the actual occurrences and any temporarily absent Lazarus species for each sample. Given the small size of DSDP samples (50 ml) and the relatively low incidence of ostracods in the deep sea, it is not possible to determine whether the temporary absence of these Lazarus species is due to sampling inadequacy or is a reflection of relatively subtle environmental changes. Whatever the cause, the author believes that what he has previously referred to as the 'cumulative species diversity' (Whatley and Coles, 1991) is a more accurate measure of diversity trends than if the Lazarus taxa are excluded.

From a very low species diversity in the lowest part of the Palaeocene sampled (NP Zone 4), there is a stepped rise to a maximum diversity peak in the middle Eocene, NP Zone 16. Both the cumulative simple species diversity and the recorded simple species diversity exhibit peaks in NP zones 6 and 8 and troughs in NP zones 7 and 9. Further sampling and an improved data base are required to substantiate whether these, and the curious peaks and troughs of NP zones 11, 12 and 14 are artefacts of sampling or genuine records of diversity fluctuation.

From a Palaeogene diversity maximum in NP Zone 16, there is a steep decline into the late middle Eocene and early upper Eocene (NP zones 17, 18, 20 and 21). After this there is an increase, albeit an irregular one with a major decline in the early upper Oligocene NP Zone 23) into the uppermost Oligocene. The upper Oligocene diversity maximum (NP Zone 25) of 97 species is, however, substantially less than the 160 species of the middle Eocene peak.

TABLE 3. THE POSSIBLE RELATIONSHIPS BETWEEN SPECIFIC AND GENERIC DIVERSITY AND NUMBER OF SAMPLES STUDIED FOR THE VARIOUS AGES

	Samples	Species	Genera	S/spp.	S/gen.
Upper Palaeocene	12	50	28	4.16	2.33
Lower Eocene	4	58	33	14.50	8.25
Middle Eocene	20	160	67	8.00	3.35
Upper Eocene	9	54	33	6.00	3.66
Lower Oligocene	4	33	20	8.25	5.00
Upper Oligocene	17	111	49	6.52	2.88

These figures are certainly to some extent influenced by the number of samples processed. A major hiatus occurs in the Southwest Pacific/ Australasian region and much of the Oligocene and upper Eocene are absent due to the corrosive effects of the cold, dense psychrospheric water which flooded into the area from the south at this time (Edwards, 1975; Kennett *et al.*, 1972, 1974; Kenneth, 1980). At some sites, such as Site 207, strata from the middle Eocene to the middle Miocene are absent due to this cause and for this reason there is a paucity of samples of this age in the study.

Table 3 indicates the possible relationships between specific and generic diversity and number of samples studied for the various ages.

This table demonstrates that whatever the relationship is between diversity and samples, it is not a simple one. The values for s/spp. and s/gen. derived by respectively dividing the number of species and genera by the number of samples for each age, clearly demonstrate this. It has not been possible to normalize any of the data for time due to the inadequacy of absolute ages available for the NP and NN zones and because of uncertainty of the exact position of most of the samples within those zones.

Figure 2b plots the number of new species recorded for each of the NP and NN zones (originations) and the number of species becoming extinct in each zone (extinctions) for the Cainozoic of the Southwest Pacific. Extinctions are calculated in terms of total final extinction of a species in the study area, rather than indicating the time of its initial disappearance as a Lazarus species. Similarly, originations mark only the first appearance of a species and not its reappearance after temporary absence.

The highest origination peak for the Palaeogene occurs in the middle Eocene in NP Zone 16. This coincides with the maximum Palaeogene diversity peak. Earlier peaks occur in NP zones 6, 8, 12 and 15. These peaks are effectively separated (and accentuated) by intervals of low levels of origination; such troughs occur in NP zones 7, 9, 11 and 14.

Throughout the Palaeocene, lower Eocene and the early middle Eocene, originations always exceed extinctions, thereby allowing species diversity to increase continually during this interval. However, in the middle Eocene NP Zone 16, extinction levels considerably exceed those for originations, notwithstanding the fact that the latter are at their highest level for the entire Palaeogene. Of the 138 species in NP Zone 16, (126 recorded plus 12 Lazarus species), no less than 48 species (34.7%) are new, while 73 species become extinct at this time, representing 52.8% of the total for the zone. With no fewer than 87.5% of its fauna being either new or becoming extinct, NP Zone 16 represents a time of huge faunal turnover. As will be discussed later, this is a phenomenon which can be observed occurring contemporaneously in other oceans, nothwithstanding the fact that other authors, notably Benson (1975, 1990) suggest that late rather than mid-Eocene times witnessed the greatest amount of faunal change in the benthonic Ostracoda of the deep sea.

From the very high levels of evolutionary activity in NP Zone 16, there is a steep decline in both origination and extinction rates to NP zones 17 and 18. Indeed, this activity becomes so reduced at this time that, at the upper Eocene/lower Oligocene boundary, there are no extinctions or originations in

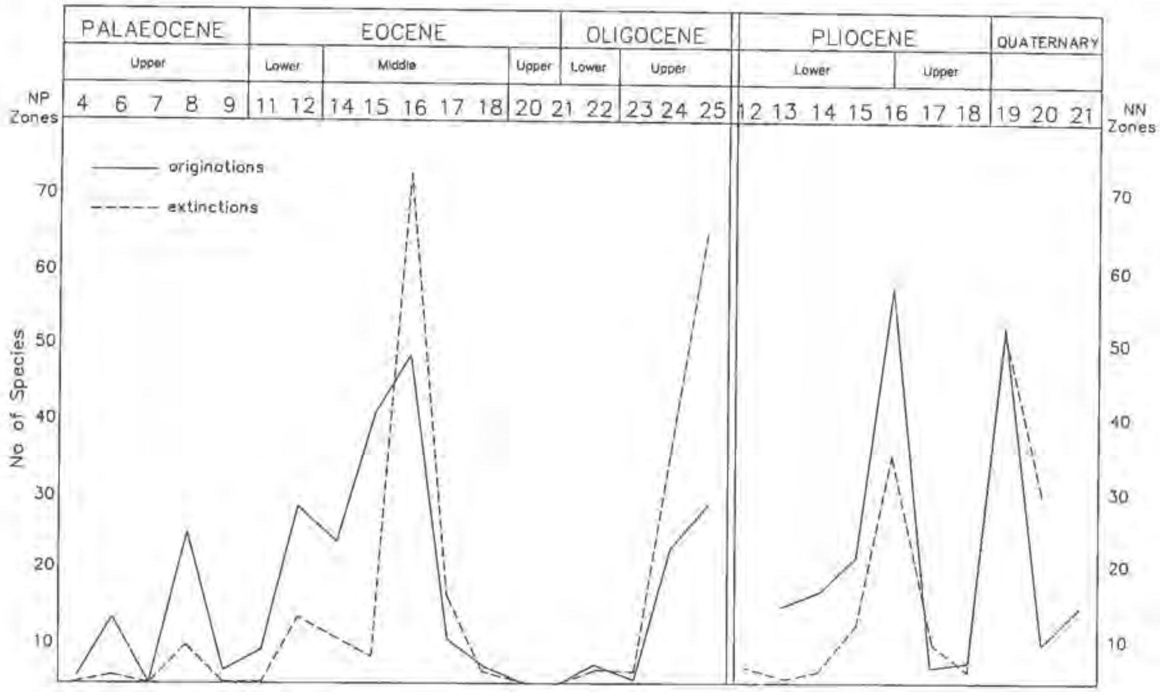

FIG. 2b. Number of new species and number of species becoming extinct *per* nannofossil zone through the Cainozoic of the Southwest Pacific.

NP zones 20 or 21 and the level remains very low in the two succeeding zones. However, there is a considerable upsurge of evolutionary activity in NP Zone 24 which is continued on into NP Zone 25. Extinction levels for this latter zone at 65 species is a very high proportion (77%) of the total number of species in the zone (84 spp), and origination rates are also high.

NEOGENE AND QUATERNARY

The data on which the following observations are based are taken from Whatley (1983); Whatley and Ayress (1988); Ayress (1988); Coles *et al.* (1990) and Downing (1985). All these studies have been carried out at Aberystwyth. These data have been produced from the analysis of 104 samples from the Pliocene and Quaternary. Additionally, 38 samples from 10 DSDP sites in the Southwest Pacific, together with five other samples of the same age collected from the Loyalty Basin, have been studied from Miocene strata. Regretably, other than the fact that they yielded an unrefined gross total of 238 species belonging to 62 genera, no other data is available from the Miocene study, except that Downing (1985) notes that of the 200 Pliocene species (gross unrefined total) she recorded from the region, 58 (29%) also occurred in the Miocene. The DSDP material studied for its Neogene and Quaternary Ostracoda is from the sites listed in table 4, many of which were also studied for their Palaeogene fauna. The unpublished Miocene study was carried out by Harlow, most of the Pliocene data is from Downing (1985) and most of the Quaternary is from Ayress (1988) who also studied some Pliocene samples. Other Quaternary data is from Dainty (1984) and Smith (1983). Coordinates and bathymetric data are given only for those sites not treated above. Data from the summit of the Ita Mai Tai guyot, DSDP Site 200, are excluded here since they are the subject of a separate forthcoming publication.

TABLE 4. STRATIGRAPHICAL AGE, NUMBER OF SAMPLES EXAMINED, PRESENT DAY WATER DEPTH, LOCALITY AND COORDINATES OF THE DSDP SITES IN THE SOUTHWEST PACIFIC

Site	Age	Locality	Coordinates		PDWDm	S
47	Pliocene	Shatsky Plateau	32°29.9'N	157°42.7'E	2,689	6
55	M. Miocene/Pliocene	Caroline Ridge	9°18.9'N	142°32.1'E	2,850	12
56	M.Miocene	Caroline Ridge	8°22.4'N	143°33.6'E	2,508	6
57	Pliocene	Caroline Ridge	8°40.0'N	141°32.0,E	3,300	6
62	M. Miocene-Pliocene	Eauripik Ridge	10°52.2'N	141°56.3'E	2,591	11
64	M. Miocene-Quaternary	Ontong Java Plateau	1°44.4'S	158°36.54'E	2,052	13
203	U. Pliocene-Quaternary	Lau-Havre Basin	22°09.22'S	177°32.7'E	2,720	6
206	Palaeocene-Quaternary	New Caledonia Basin	22°09.22'S	177°32.7'E	2,720	6
206	Palaeocene-Quaternary	New Caledonia Basin			3,196	13
207	U. Cretaceous-Quaternary	Lord Howe Rise			1,389	14
208	U.Cretaceous-Quaternary	Lord Howe Rise			1,545	11
209	M. Eocene-Quaternary	Queensland Plateau			1,428	13
277	Palaeogene,Quaternary	Campbell Plateau			1,214	3
279	Quaternary	Tasman Ridge	51°20.14'S	162°38.10'E	3,341	4
281	Quaternary	South Tasman Rise	47°59.84'S	147°45.85'E	1,591	4
282	Quaternary	Tasman Rise	42°14.67'S	143°29.18'E	4,202	3
284	Quaternary	Challenger Plateau	40°30.48'S	167°40.81'E	1,066	5
288	M. Miocene-Pliocene	Ontong Java Plateau	5°38.38'S	161°41.53'E	3,000	4
289	U. Cretaceous-Quaternary	Ontong Java Plateau			2,206	

The gross stratigraphical distribution of the samples is given in table 5.

The simple species diversity of the Ostracoda in the Neogene and Quaternary is given in figure 2a. As previously mentioned, the only data for the Miocene is that Harlow recovered a total of 238 species from 53 samples, mainly from the middle Miocene. Given that Downing recovered only 200 species from 61 samples, mostly at the same sites, this suggests that mean Miocene diversity levels were probably higher than those for the Pliocene. The Pliocene in the Pacific, as elsewhere in the world oceans, seems to register a decline in its ostracod diversity as will be discussed later. This is emphasized in a very crude manner in table 6 based on the unrefined total recovery of species *per* Era from all the studies undertaken at Aberystwyth and not normalized for geological time (see table 6).

Figure 2a shows a steep increase in diversity from the lowest point of cumulative species diversity (79 species) in NN Zone 12 in the lower Pliocene, to a strong peak with 171 cumulative species in NN Zone 16 which spans the lower/upper Pliocene boundary. This peak is followed by a decline through NN Zone 17 to a trough in NN Zone 18 in the uppermost Pliocene which is immediately followed by another steep rise to NN Zone 19 in the early Quaternary. This latter peak in the graph of cumulative simple species diversity, with 193 species, represent the diversity high point for Pacific deep sea Ostracoda. Placed in an overall Cainozoic perspective, it is 71% higher than in NP Zone 16 Palaeogene peak of 138 species in the middle Eocene and 36% higher than that of the preceeding Pliocene peak. From this diversity peak there is a steep diversity decline to NN zones 20 and 21 in the subsequent Quaternary with a cumulative total of 141 and 125 species respectively.

Without question, as tables 4 and 5 show, there is

TABLE 5. DISTRIBUTION IN TIME OF NEOGENE AND QUATERNARY SAMPLES FROM THE SOUTHWEST PACIFIC

	Samples
Quaternary	50
Pliocene	54
Miocene	44

TABLE 6. DISTRIBUTION OF OSTRACOD SPECIES BY AGE THROUGH THE CAINOZOIC OF THE SOUTHWEST PACIFIC

Age	Species
Quaternary	365
Pliocene	200
Miocene	238
Oligocene	118
Eocene	202
Palaeocene	50

a degree of relationship between variation in diversity and in the number of samples studied.

The rate of evolutionary turnover, as measured by the number of species originating or becoming extinct in each of the NN zones of the Pliocene and Quaternary is given in figure 2b. This graph closely mirrors that of simple species diversity for the same interval (Fig. 2a), in that there are two major peaks, in both parameters measured, in NN zones 16 and 19, respectively.

Originations are at a very low level in the early Pliocene and rise only very gradually to NN Zone 15. However, the subsequent rise to NN zone 16 is very steep and the number of originations is more than doubled; from 23 to 58. The number of newly appearing species then crashes to only 4 in the succeeding zone, remains low (5) in the next, but again rises very steeply into NN Zone 19 where there are 53 originations. There follows a steep drop to NN Zone 20 (10) with a slight increase into NN Zone 21 (15).

The extinction curve closely follows that of originations. Extinctions are very low in the first four zones of the Pliocene but increase sharply into NN Zone 16, where 36 species appear for the last time. There is then a steep decline into the two subsequent zones with 10 and 3 extinctions respectively. However, in NN Zone 19 occurs the highest level of extinction since the Oligocene with 52 species; only 30 extinctions occur in NN 20.

The mid-Pliocene (NN Zone 16) and the early Quaternary (NN Zone 19) were obviously times of very high evolutionary activity. In the former, based on the cumulative simple species diversity, only 46% of its fauna did not originate in the zone or become extinct in it. In the latter, only 27% of the ostracods appeared for the first or last time.

COMPARISON WITH OTHER OCEANS

With respect to both variations in specific diversity and origination/extinction rates, there are considerable similarities with the faunas of other oceans. However, while when there is a coincidence in these measured phenomena it is suggestive of causation by global wide factors, where there is a divergence, other causes must be sought.

Benson (1990) suggests that there were five major global palaeoceanographical 'events' during the last 80 Ma which were discovered by studies of the diversity and evolution of deep sea Ostracoda. These events are: **1.** The K/T boundary extinction event at 65 Ma; **2.** The 40-38 Ma event during the late Eocene with the establishment of the psychrosphere and the thermocline due to the generation of cold dense water in the Antarctic; **3.** The 16-14 Ma middle Miocene event, with changes in the Indo-Pacific and South Atlantic faunas, the formation of the East Antarctic Ice Cap and the closure of the southeastern end of Tethys; **4.** The 6.3-4 Ma event at the end of the Miocene, coinciding with an Antarctic glacial maximum and the closure of the Iberian Portal leading to the Messinian Salinity Crisis; **5.** The 3.5 Ma event during the Pliocene related to the closure of the Straits of Panamá and further decline in ocean temperatures.

Whatley and Coles (1991) and Coles (1990) have shown in the North Atlantic, as in the Pacific, that the diversity of the Palaeocene deep sea ostracod fauna is low, relative both to the subsequent Cainozoic and the preceeding Maastrichtian (Whatley, 1986, 1988, 1990). In both instances, however, the diversity level recorded may be artificially low due to inadequate sampling.

In the Pacific, as can be clearly seen in figures 2a and 2b, the acme of evolutionary activity occurs, not in the late Eocene but in the middle part of the middle Eocene in NP Zone 16. It may be argued, however, that the extremely low diversity and evolutionary rate of the late middle Eocene, upper Eocene and lowermost Oligocene are not simply the result of

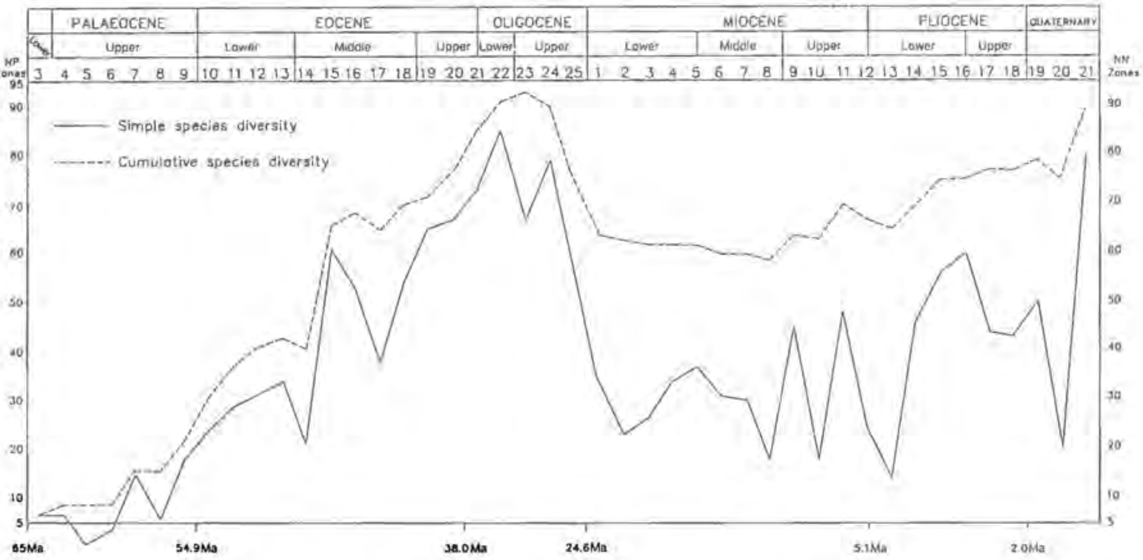

FIG. 3a. Single species diversity and cumulative species diversity of Cainozoic deep sea Ostracoda in the North Atlantic.

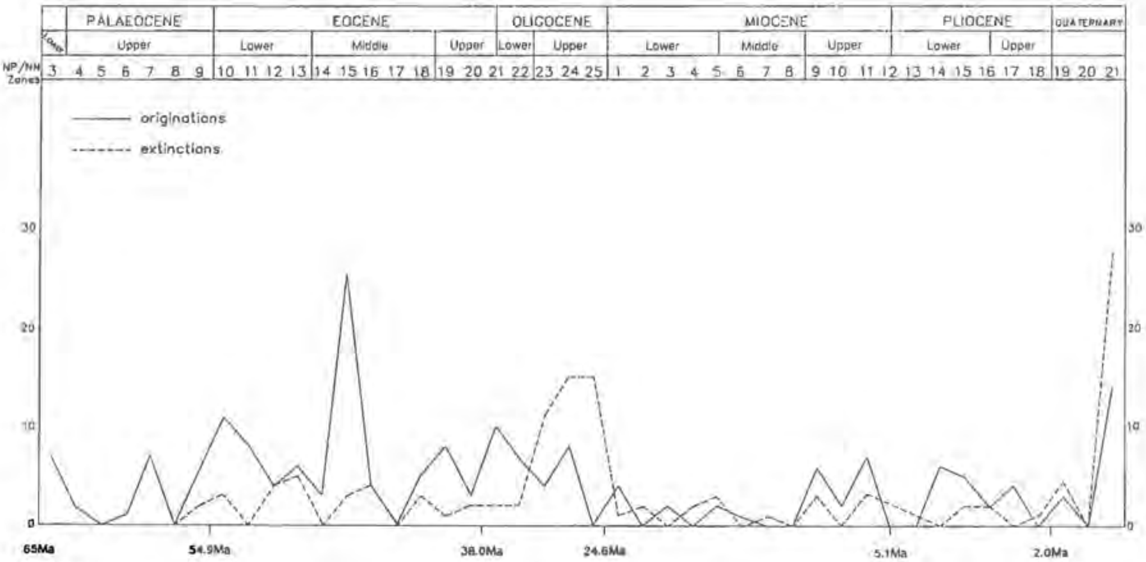

FIG. 3b. The number of new species and the number of species extinction *per* nannofossil zone through the Cainozoic of the North Atlantic.

paucity of sampling in the Pacific where so much strata has been removed by the incoming psychrospheric water, but that this water was cold enough to be inimical to ostracods at this time. What is important to recognize, however, is that with such low extinction and origination rates in the 40-38 Ma interval, there seems not to have been such a large faunal changeover as has sometimes been suggested.

It is interesting to note that in the North Atlantic (Figs. 3a, 3b) there is only a very slight diminution in simple species diversity after a middle Eocene peak (NN Zone 15) and almost immediately diversity increase again to peak in the upper Oligocene (Whatley and Coles, 1991). Clearly no case can be made for a 40-38 Ma event in the North Atlantic and Benson (1990) concedes this. Possibly the cold psychrospheric water did not reach the North Atlantic until considerably later than the Southwest Pacific. Figure 3a, taken from Whatley and Coles (1991) shows the recorded and cumulative simple species diversity for the Cainozoic of the North Atlantic and the late Oligocene/early Miocene diversity crash may possibly be correlated with the arrival of this cold water. Comparing figures 2a and 3a, it can be seen that Pacific late Oligocene diversity is increasing while that of the Atlantic is falling.

There is no evidence from figures 2a, b and 3a, b to support Benson's 3rd and 4th events, both of which take place in the Miocene. However, figures 2a and 3a show that lower Pliocene diversity is rather low and figures 2b and 3b illustrate that evolutionary activity was also low at the time. This could have been brought about by end Miocene glacial maxima in the Antarctic and was possibly also influenced by tectonic events in the Western Tethys, although quite what the consequences of the latter would be with respect to southwestern Pacific faunas is uncertain.

The Pliocene witnessed dramatic diversity and taxonomic changes in the southwest Pacific, with a mid-Pliocene (NN Zone 16) peak in both diversity and origination/extinction rates, preceeded and succeeded by troughs (Figs. 2a, 2b). There is a similar peak in recorded simple species diversity in the North Atlantic in NN Zones 16 as shown in figure 3a. This possibly relates to the Pliocene event (number 5) of Benson; certainly the mid-Pliocene was a relatively warm interval sandwiched between cooler episodes and this may be reflected in the observed faunal changes in both oceans.

In the Pacific the diversity peak for the Quaternary occurs in the early Pleistocene NN Zone 19 and it is in this zone that peaks of both extinctions and originations also occur. Unpublished data available to the author indicates that, in the Indian Ocean, the simple species diversity peak also occurs in NN Zone 19, as shown in figure 4a. Unlike the Pacific, however, where the diversity is 4/5 less in NN Zone 20 and only a little recovered in NN Zone 21, in the Indian Ocean, there is only a small diversity decline into NN Zone 20 and not a much greater decline into NN Zone 21. Also contrasting is the fact that although early Pleistocene originations are high in the Indian Ocean, they actually fall from a late Pliocene (NN Zone 18) peak (Fig. 4b). A further distinction is the fact that there is no coincidence between origination and extinction levels in the Quaternary of the Indian Ocean; the former peak in NN Zone 19 and the latter in NN Zone 20.

In the North Atlantic, as shown in figure 3a, cumulative species diversity increases gradually throughout the Pliocene, declines somewhat from NN Zone 19 to NN Zone 20 but increases to a Quaternary maximum in NN Zone 21. Whatley and Coles (1991) have shown that originations and extinctions are low in the North Atlantic in NN Zone 19, that none occur in NN Zone 20 but that both rise (extinction twice as sharply) to Quaternary peaks in NN Zone 21 (Fig. 3b).

With respect to the Quaternary, the more dramatic vissisitudes suffered by the deep Ostracoda in the Indian and Pacific Oceans are possibly related to the fact that, as the Pleistocene advanced, they reacted more adversely as did shallow water low latitude biotas (McGhee, 1989), to global cooling than did those in the higher latitudes of the North Atlantic. In the case of the deep water benthos, this is more likely to have been an indirect effect associated with perturbations to oceanic plankton systems in the surface layers.

DISCUSSION

The fact that different faunal responses are recorded in different oceans is sometimes a reflection of different responses to the same event, such as the different reactions cited above to progressive climatic

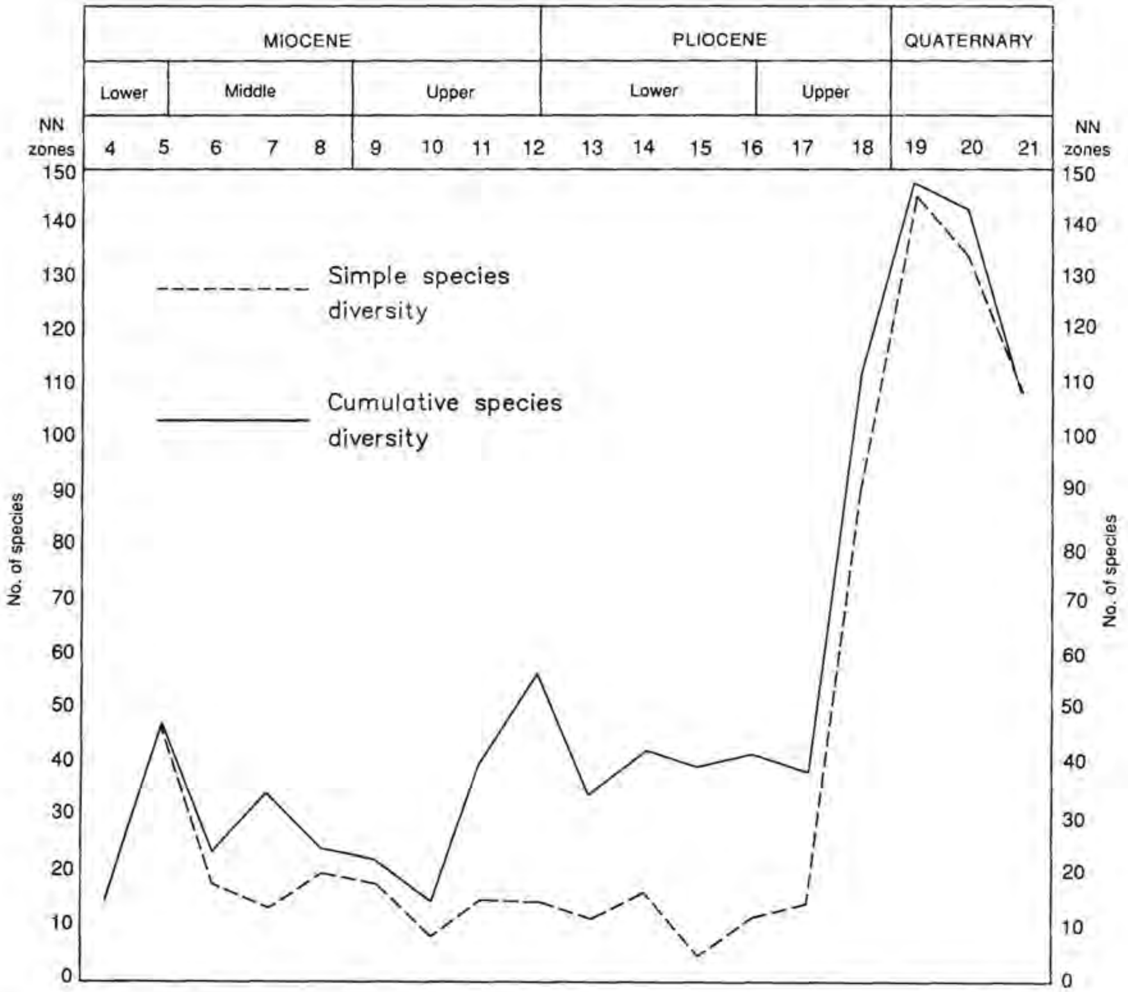

FIG. 4a. Simple species diversity and cumulative species diversity of Cainozoic deep water Ostracoda in the Indian Ocean.

deterioration. It is also likely that, while some effects may be detected globally, in many instances, the consequences of such events as the opening of the Drake Passage, the closure of the Strait of Panamá or of the Iberian Portal, will be most strongly felt in those areas in greatest proximity. Also, there is likely to be a time lag effect in that those areas most geographically distant will suffer both temporarily retarded and reduced impact consequences.

It is important to remember both of these factors when attempting to correlate events in the deep sea on the basis of their consequences to biotic evolution. The major difference between late Paleogene ostracod evolution in the southwest Pacific and North Atlantic and its possible relationship to the time lag effect of the inception of the psychrosphere in these areas, is an excellent example of this.

Largely ignored by most authors, however, is the fact that not all the peaks and troughs on our graphs are occasioned by extrinsic factors such as global, regional or local environmental perturbations. Of equal importance are the faunal changes brought about by background evolution. Whether or not this background level is periodically accelerated by 'events', its continual and uninterrupted contribution to the turnover of faunas is always underated. While the many environmental perturbations which took place in the 65 Ma Tertiary history of the Pacific deep sea Ostracoda may have hastened the extinction of certain taxa and enhanced the survival prospects of

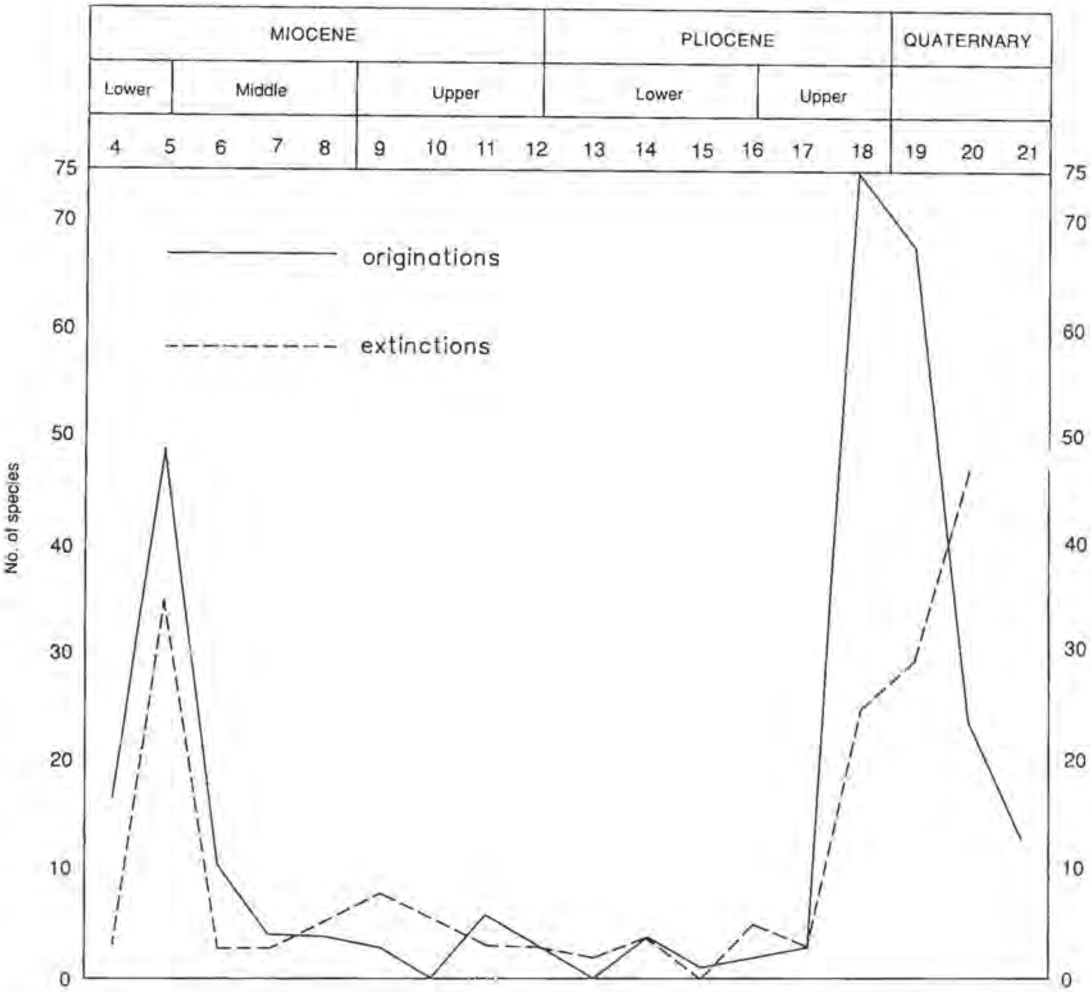

FIG. 4b. The number of new species and the number of species extinction *per* nannofossil zone through the Cainozoic of the Indian Ocean.

others, it should not be forgotten, and this is the case particularly post the establishment of the two-layered ocean, that environmental conditions on the deep sea flow are, relatively speaking, very stable. The insulating effects of thousands of metres of sea water must have created conditions where evolution, governed mainly by what we have come to call the Red Queen set of rules, could proceed unmolested by numerous small scale environmental changes.

The very substantial differences between those faunas which make up the modern deep sea ostracod fauna of the World Ocean compared to those of, for example, the Palaeogene, bear witness to the significance of this change. Whatley (1983) gives some data on the compositional changes in the fauna with time but these remain inadequate. The author's intention was to include more data here but space does not permit. This must await a subsequent study.

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REFERENCES

Angel, M.V. 1968. The thermocline as an ecological boundary. *Sarsia*, No.34 p. 299-312. London.

Ayress, M.A. 1988. Late Pliocene to Quaternary deep-sea Ostracoda from the eastern Indian and southwestern Pacific Ocean. Ph.D. Thesis (Unpublished), *University of Wales*, 1088 p. Aberystwyth, United Kingdom.

Benson, R.H. 1975. The origin of the psychrosphere as recorded in changes in the deep-sea ostracode assemblages. *Lethaia*, Vol. 8, No. 1, p. 69-83.

Benson, R.H. 1990. Ostracoda and the discovery of global Cainozoic palaeoceanographical events. *In* Ostracoda and global events (Whatley, R.C.; Maybury, C.A.; editors). *Chapman and Hall*, p. 41-58. London.

Benson, R.H.; Chapman, R.E.; Deck, L.T. 1985. Evidence from the Ostracoda of major events in the South Atlantic and worldwide over the past 80 million years. *In* South Atlantic Paleoceanography (Hsu, K.J.; Weissert, H.J.; editors), *Cambridge University Press*, Ch. 16, p. 325-350.

Coles, G.P. 1989. Cainozoic evolution of Ostracoda from deep waters of the North Atlantic and adjacent shallow water regions. Ph.D. Thesis (Unpublished), *University of Wales*, 1199 p. Aberystwyth, United Kingdom.

Coles, G.P. 1990. A comparison of the evolution, diversity and composition of Cainozoic Ostracoda in the deep water North Atlantic and shallow water environments of eastern North America and Europe. *In* Ostracoda and Global Events (Whatley, R.C.; Maybury, C.A.; editors). *Chapman Hall*, p. 71-86. London.

Coles, G.P.; Whatley, R.C. 1989. New Paleogene to Miocene genera and species of Ostracoda from Deep Sea Drilling Project sites in the North Atlantic. *Revista Española de Micropaleontología*, Vol. 21, No. 1, p. 81-124.

Coles, G.P.; Ayress, M.A.; Whatley, R.C. 1990. A comparison of North Atlantic and Pacific Cainozoic deep sea Ostracoda. *In* Ostracoda and Global Events (Whatley, R.C.; Maybury, C.A.; editors). *Chapman and Hall*, p. 287-306. London.

Dainty, E.J. 1984. The taxonomy, biostratigraphy, and palaeoecology of the Pleistocene Ostracoda obtained from four Deep Sea Drilling Project Sites in the South West Pacific. M.Sc. Thesis (Unpublished). *University of Wales*, 411 p. Aberystwyth, United Kingdom.

Downing, S.E. 1985. The taxonomy, palaeoecology, biostratigraphy and evolution of Pliocene Ostracoda from the W. Pacific. Ph.D. Thesis (Unpublished), *University of Wales*, 1073 p. Aberystwyth, United Kingdom.

Edwards, A.R. 1975. Southwest Pacific Cenozoic paleogeography and an integrated Neogene paleocirculation model. *In* Proceedings of the Ocean Drilling Program, Peru continental margin, Leg 112 (Suess, E. *et al.*; editors). *College Station, Initial Reports*, Vol. 30, p. 667-684. Washington.

Galehouse, J.S.; Packham, G.H.; Van der Lingen, G.J. 1972. Australian-Antarctic continental drift paleocirculation changes and Oligocene deep-sea erosion. *Nature; Physical Science*, Vol. 239, No. 91, p. 51-55.

Kennett, J.P. 1973. Middle and late Cenozoic planktonic foraminiferal biostratigraphy of the Southwest Pacific, DSDP, Leg. 21. *In* Proceedings of the Ocean Drilling Program, Peru continental margin, Leg 112 (Suess, E. *et al.*; editors). *College Station, Initial Reports*, Vol. 21, p. 575-639. Washington.

Kennett, J.P. 1980. Palaeoclimatography and biogeographic evolution of the Southern Ocean during the Cenozoic, and Cenozoic microfossil datums. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Vol. 31, Nos. 2-4, p. 123-152.

Kennett, J.P.; Burns, R.E.; Andrews, J.E. ; Churkin, M. Jr.; Davis, T.A.; Dumitrica, P.; Edwards, A.R.; Calehouse, J.S.; Packham, G.H.; van der Lingen, G.J. 1972. Australian-Antarctic continental drift, palaeocirculation changes and Oligocene deep-sea erosion. *Nature; Physical Science*, Vol. 239, No. 91, p. 51-55.

Kennett, J.P.; Houtz, R.E.; Andrews, P.B.; *et al.* 1974. The development of the Circumantarctic Current. *Science*, Vol. 186, p. 144-147.

McGhee, G.R. 1989. Catastrophes in the History of Life. *In* Evolution and the Fossil Record (Allen, K.; Briggs, D.; editors). *Belhaven Press*, p. 26-50. London.

Millson, K.J. 1988. The palaeobiology of Palaeogene Ostracoda from Deep Sea Drilling Project cores in the South West Pacific. Ph.D. Thesis (Unpublished), *University of Wales*, 733 p. Aberystwyth, United Kingdom.

Smith, P.D. 1983. Quaternary deep-sea Ostracoda from the Southwest Pacific. Ph.D. Thesis (Unpublished), *University of Wales*, 254 p. Aberystwyth, United Kingdom.

Steineck, P.L.; Dehler, D.; Hoose, E.M.; McCalla, D. 1988. Oligocene to Quaternary ostracods of the central Equatorial Pacific (Leg 85, DSDP-IPOD). *In* Evolutionary biology of Ostracoda; its fundamentals and applications (Hanai, T.; Ikeya, N.; Ischizaki, K.; editors). *International Symposium on Ostracoda, No. 9 (1985), Proceedings*, p. 597-617.

Whatley, R.C. 1983a. Some aspects of the palaeobiography of Tertiary deep-sea Ostracoda from the S.W. Pacific. *Journal of Micropalaentology*, Vol. 2, p. 83-104.

Whatley, R.C. 1983b. Evolution of the ostracods *Bradleya* and *Poseidonamicus* in the deep-sea Cainozoic of the South-West Pacific. *Special Papers in Palaeontology*, No. 33, p. 103-116.

Whatley, R.C. 1986. Biological events in the evolution of Mesozoic Ostracoda. *In* Lecture Notes in the Earth Sciences, No. 8, Global Bio-Events (Walliser, D; editor). *Springer Verlag*, p. 140-147.

Whatley, R.C. 1988. Patterns and rates of evolution in Mesozoic Ostracoda. *In* Evolutionary biology of Ostracoda; its fundamentals and applications. (Hanai, T.; Ikeya, N.; Ischizaki, K.; editors). *International Symposium on Ostracoda, No. 9 (1985), Proceedings*, p. 1021-1040. Shizuoka, Japan.

Whatley, R.C. 1990a. Ostracoda and Global events. *In* Ostracoda and Global Events (Whatley, R.C.; Maybury, C.A.; editors). *Chapman and Hall*, p. 3-24. London.

Whatley, R.C. 1990b. The relationship between extrinsic and intrinsic events in the evolution of Mesozoic nonmarine Ostracoda. *In Symposium on Bio-Events, No. 2 (1987), IGCP, No. 216, Mesozoic Extinction Events, Proceedings*, p. 253-263. Bilbao.

Whatley, R.C. (In press). The reproductive and dispersal strategies of Cretaceous nonmarine Ostracoda: the key to pandemism. *In International Symposium on nonmarine Cretaceous Correlations, No. 1 (1987), IGCP No. 245, Proceedings*. Uromqui, China.

Whatley, R.C.; Uffenorde, H.; Harlow, C.J.; Downing, S.E.; Kesler, K.J. 1982. The Rockalliidae; a new family of Cytheracean Ostracoda. *Journal of Micropalaeontology*, Vol.1, p. 1-11.

Whatley, R.C.; Harlow, C.J.; Downing, S.E.; Kesler, K.J. 1983. Some observations on the origin, evolution, dispersion and ecology of the genera *Poseidonamicus* Benson and *Bradleya* Hornibrook. *In* Applications of Ostracoda to economic and scientific problems, programs and abstracts (Maddocks, R.F.; editor). *International Symposium on Ostracods, No. 8, Proceedings*, p. 51-77. Houston.

Whatley, R.C.; Ayress, M.A.; Downing, S.E.; Harlow, C.J.; Kesler, K.J. 1985. *Aratrocypris*, an enigmatic new deep-sea cyprid ostracod from the Tertiary and Quaternary of the Southwest Pacific. *Journal of Micropalaeontology*, Vol. 4, No. 2, p. 69-79.

Whatley, R.C.; Ayress, M.A.; Downing, S.E. 1986. Two unusual new species of the ostracod genus *Cytheropteron* from the late Cainozoic of the deep sea. *Journal of Micropalaeontology*, Vol. 5, No. 1, p. 31-36.

Whatley, R.C.; Coles, G.P.1991. Global change and the biostratigraphy of North Atlantic Cainozoic deep water Ostracoda. *Journal of Micropalaeontology*, Vol. 9, No. 2, p. 119-132.

Whatley, R.C.; Downing, S.E.; Harlow, C.J.; Kesler, K.J. 1987. New species of the ostracod genus *Poseidonamicus* from the deep sea Cainozoic of the southwest Pacific. *Revista Española de Micropaleontología*, Vol. 18, No. 3, p. 387-400.

Whatley, R.C.; Ayress, M.A. 1988. Pandemic and endemic distribution patterns in Quaternary bathyal and abyssal Ostracoda. *In* Evolutionary biology of Ostracoda; its fundamentals and applications. (Hanai, T.; Ikeya, N.; Ischizaki, K.; editors). *International Symposium on Ostracoda, No. 9 (1985), Proceedings*, p. 1003-1020. Kodansha-Elsevier.

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