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Taxonomic diversity of Late Cenozoic Cytheroidea (Ostracoda) from Cyprus Island

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KEY WORDS – Ostracoda, Late Cenozoic, Cytheroidea, Taxonomic Diversity Indices, Cyprus, Palaeoecology, Messinian Salinity Crisis.

ABSTRACT - Late Cenozoic ostracod assemblages of south-western Cyprus offer a unique opportunity to document the faunal changes which occurred at various marine sites during the Upper Miocene–Lower Pliocene around the island coast. Previously, biostratigraphic data based on Ostracoda fauna obtained from Kalavassos and Nicosia Formations pointed to strong environmental changes that presumably are related to the so-called “Messinian Salinity Crisis” event. This information is compared to those restricted on 10 samples belonging to three sections, Amargeti, Polemi, and Mari and the changes in the Cytheroidea taxocenosis documented through a qualitative analysis of the ostracod material. For the first time two indices of diversity, the Average Taxonomic Distinctness (called Delta+ index) and the Variation of Taxonomic Distinctness (the Lambda+ index) are used for the characterisation of changes in fossil ostracod assemblages. Information on Cytheroidea assemblages was used for three levels of the Linnaean hierarchy (the species, the genus, and the family), following the Clarke and Warwick (1998, 2001) algorithms for the computation of the taxonomic diversity. The results suggest the occurrence of stressful ecological conditions in the coastal environment during a short period of time, more precisely during a lowering of the marine water level where the sampling area transformed in an environment with brackish lagunar conditions, followed later-on by the reversal to an eumarine situation. It is concluded that the Clarke and Warwick taxonomic diversity indices are useful descriptors for palaeoecological changes and should be more widely used.

RIASSUNTO – [Diversità tassonomica dei Cytheroidea (Ostracoda) dell'isola di Cipro] – Tra il Miocene superiore ed il Pliocene inferiore, in diverse località della costa sud-occidentale dell'isola di Cipro si verificarono importanti cambiamenti faunistici. Lo studio delle associazioni fossili ad ostracodi di queste località offre un'opportunità unica per studiare le variazioni paleoambientali. I dati biostratigrafici ottenuti dallo studio delle ostracofaune delle formazioni Kalavassos e Nicosia hanno fornito indicazioni di importanti variazioni ambientali, presumibilmente collegate alla cosiddetta “Crisi di salinità del Messiniano”. Si è cercato di verificare l'evento su 10 campioni provenienti da tre diverse sezioni stratigrafiche: Amargeti, Polemi e Mari; i cambiamenti nelle associazioni tassonomiche a Cytheroidea sono stati documentati per mezzo di un'analisi qualitativa delle ostracofaune stesse. Per la prima volta vengono qui utilizzati, per caratterizzare i cambiamenti delle associazioni ad ostracodi, due indici di diversità: la Distinzione Tassonomica Media (detta anche indice Delta+) e la Variazione di Distinzione Tassonomica (indice Lambda+). Le informazioni sulle associazioni a Cytheroidea sono state utilizzate per tre livelli della gerarchia linneiana (la specie, il genere e la famiglia), seguendo gli algoritmi di Clarke e Warwick (1998, 2001) per calcolare la diversità tassonomica. I risultati suggeriscono la presenza di condizioni ecologiche “stressate” nell'ambiente costiero durante un breve periodo di tempo, più precisamente durante un abbassamento del livello del mare. L'area campionata si sarebbe trasformata in un ambiente lagunare salmastro, successivamente ritornato a condizioni francamente marine. Si conclude che gli indici di diversità tassonomica di Clarke e Warwick siano strumenti di grande utilità per descrivere i cambiamenti paleoambientali, e dovrebbero essere usati più ampiamente per le ricostruzioni paleoecologiche.

INTRODUCTION

Late Cenozoic (Upper Miocene–Lower Pliocene) ostracod assemblages of Cyprus offer a unique opportunity to document the faunal changes which occurred at various marine sites during the so-called “Messinian Salinity Crisis” event. One should recall that the Miocene ended in the Mediterranean space, with the desiccation of wide areas and the deposition of huge amount of salts (Duggen *et al.*, 2003). A chain of shallow lakes, so-called “lago-mare”, with diverse salinity conditions, from hypo- to hyper-saline ones, developed in many parts of the pre-existing sea. Giuliano Ruggieri recognised that the occurrence of *Congerina* and *Melanopsis* molluscs during this period could be related to the formation of shallow hypohaline lakes in the Palaeo-Mediterranean space at a sea-level niveau below those of the Atlantic (e.g. Ruggieri, 1958, 1967; Ruggieri & Sprovieri, 1976). More geological and palaeontological evidence appeared later on which

confirmed Ruggieri's view. For instance evidence from the ostracod fauna, e.g. the occurrence of the *Cyprideis torosa* Jones corroborates the desiccation model of the Palaeo-Mediterranean (Benson, 1976a, b) and the explanation of this catastrophic event was further documented for the closure of the connections with the Atlantic (Hsü *et al.*, 1973; Benson, 1976a). Short time later, in Early Pliocene, the ongoing plate tectonic collision of Africa and Europe allowed the influx of oceanic water via Gibraltar in this desiccated basin, filling it again. This led to the formation of the present day Mediterranean (Hsü *et al.*, 1978). A high number of publications appeared during the last 40–50 years in order to understand and bring closer to our eyes that unique phenomenon. Great attention has been paid to the study of fossil ostracods, among other organisms in order to reconstruct the environmental changes and the evolutionary palaeobiogeography of the Mediterranean realm (e.g. Russo, 1968; Benson & Sylvester-Bradley, 1971; Benson, 1976b, 1984;

Benson *et al.*, 1991; Sissingh, 1972; Gliozzi *et al.*, 2002).

Authors like G. Ruggieri and R.H. Benson used selected ostracod species as markers for the characterisation of the "Iago-mare" event (Ruggieri, 1967; Benson, 1976b). Others like Carbonnel (1978) or Gliozzi *et al.* (2002) used entire species lists with characteristic species, which could document through their origin and palaeobiogeography the transformation of an eumarine environment in different perimarine environments. Moreover R.H. Benson reconstructed historical events in the Mediterranean from the examination of morphological changes of the ostracod carapaces of selected species (Benson, 1977).

In the present contribution, we propose another type of information, the changes within the taxonomic diversity of a marine taxocenosis, the important ostracod group Cytheroidea, in time and space. Our approach is a combination between "classic" micropalaeontological studies and a statistical approach developed recently by K.R. Clarke and R.M. Warwick (Clarke & Warwick, 1998, 2001). Below we review first, conceptual and methodological aspects related to the ostracod usage for the reconstruction of the "Messinian Salinity Crisis"; we further present geological and palaeontological information on Cyprus material obtained and processed by one of us (SG) and presented in details in Galoukas (1995). The Cytheroidea data is then treated statistically for the calculation and the representation of the data with two diversity indices, the Delta+ and the Lambda+ of Clarke & Warwick (1998, 2001) in order to check how well these indices can inform us about the environmental changes already perceived by the paleontological information which already exist (Galoukas, 1995) and here briefly exposed. Finally, we discuss the advantages to combine "traditional" techniques commonly used by palaeontologists with those developed by neontologists for palaeoecological and palaeobiogeographical reconstructions.

CONCEPTUAL AND METHODOLOGICAL ISSUES

The 1967 publication of Giuliano Ruggieri became a standard reference for the idea that during the Upper Messinian, the evidence of dilute saline environments in what we call now the Palaeo-Mediterranean sea represented, as compared to the former or latter events, a period of environmental crisis (Benson, 1982, 1984; Russo, this volume). Benson's definition of what a crisis should be has to be quoted in its entirety: "a turning point in the functional progress of a system, under conditions of unusual stress, when further change brings either restoration of normal conditions or a collapse of the system" (Benson 1976a, p. 3). This author further notes in his publication that: "the concept of crisis is diagnostic...it requires value judgements about progress, normality, unusual stress...". The latter two concepts pertain to the dynamics of

organismal and/or super-organismal entities, like the behaviour of individuals within populations and/or species within a given taxocenosis with clear phylogenetical relatedness. Continuing this line of thinking Benson (1976a, p. 6) proposed to approach the concept of crisis through "biodynamic strategies from specific problems". For this scientist the study of changes in living systems is "biodynamics" in the same way that a study of changes in geological structures is "geodynamics". Biodynamics can be approached at an organismal level by the examination of structural changes, which could occur during evolutionary time or at the super-organismal level, with changes within animal assemblages. Both are related to the external environmental evolution experienced by the organisms.

Benson (1976b, p. 149), following Ruggieri's views, formulated a precise diagnostic for the biodynamic changes which reflect an environmental crisis: "The occurrence of *Cypriideis* in the Messinian indicates a strong departure from normal marine conditions, a very strong but not total dominance of continental freshwater conditions". Two other criteria were offered further in this publication (Benson, 1976b, p. 150): "If the crisis was real, there should have been an interruption in the normal rate of evolution of ostracode species and more important in the composition of their faunal assemblages". For the former argument Benson published detailed studies on species belonging to various phylogenetical lineages, e.g. the *Oblitacythereis* case (Benson, 1977). An interruption in the morphological continuity of these lineages during the Messinian as compared to the previous time situation or after the Messinian was evidenced. At the assemblage level a strong reorganisation of the species composition was documented (review in Gliozzi *et al.*, 2002). This is represented by the reduction in the typical marine ostracod lineages, which existed during the pre-Messinian in the Palaeo-Mediterranean sea and the arrival of caspi-brackish elements from the Paratethys.

August Thienemann, one of the prominent limnologists and biogeographers of the 20th century, proposed several ecological rules, called "biozoenotische Grundprinzipien" (Thienemann, 1954). We will here mention two of them: (1) the species richness is highest in habitats with strong environmental heterogeneity; (2) biotopes with strong departure from their "normal" ecological conditions and notorious biological stress lead to a local reduction in the diversity of species assemblages and a numerical increase of individuals for few dominant taxa. The generality of these principles are well documented (Krebs, 1972) and could be nowadays called the Thienemann's rules. They will be helpful in the present palaeoecological context to interpret the ostracod data presented below.

The study of complex changes within large land- or hydroscares forms nowadays the domain of Macroecology (Brown, 1995). The diversity of animal assemblages within such ecosystems can be defined by

the statistical properties of the ensemble. For instance, the individual frequencies of animal species are related to the number of species in the assemblages and these relationships can be represented through probabilistic mathematical models and various statistical expressions known as diversity indices. The Simpson's Index is one of the well-known diversity metrics also used for fossil ostracods (Pokorny, 1971). The index measures the heterogeneity of animal assemblages, and it expresses the probability that two individuals picked at random belong to same species. Diversity indices can be used at various levels of the taxonomic hierarchy, from the species level to the suprageneric ones (Tokeshi, 1999). For the reconstruction of the ostracod diversification during the evolutionary time, Whatley (1990) used the taxonomic diversity of the main phylogenetic groups, the Cytheroidea and the Cypridoidea. Whatley's approach was to represent the numbers of taxa for various levels of the Linnean hierarchy, i.e. the species, genus and family levels. During the last years it became evident that a better representation of the diversity of animal assemblages can be achieved through the integration of phylogenetic information (Webb *et al.*, 2002). Unfortunately for many animal groups phylogenetic reconstructions are lacking; in such cases the usage of Linnean hierarchic systems for the computation of taxonomic diversity can be still very helpful (Robeck *et al.*, 2000).

Clarke & Warwick (1998, 2001) proposed as a taxonomic diversity index the Average Taxonomic Distinctness (AvTD or Delta+) which measures the average length of the taxonomic path between any two randomly chosen species (i, j):

$$(AvTD) = \text{Delta+} = [(\sum_{i < j} \omega_{ij}) / (s(s-1)/2)]$$

where s = number of species present and the ω_{ij} is the

taxonomic distance or distinctness weight. The average taxonomic distinctness or diversity can be seen as a generalisation of Simpson's diversity index (Warwick & Clarke, 2001). This index allows comparisons between presence/absence of species in assemblages. We use here species lists for characterisation of an assemblage following the idea of Botkin *et al.* (1979). These authors pointed out that a species list encapsulates enough information, which can characterise species assemblages or can give us information on the structure of ecosystems. Warwick & Light (2002) point out that species lists of the "spatially averaged" death assemblages of molluscs in Britain reflect well the living assemblages of the surrounding sampling area. Hence we consider that the ostracod lists we will use in this study are representative of the ostracod assemblages which existed during various geological periods.

Variation in Taxonomic Distinctness (VarTD or Lambda+) measures the evenness of the taxonomic structure in an assemblage (Clarke & Warwick, 2001; Warwick & Clarke, 2001):

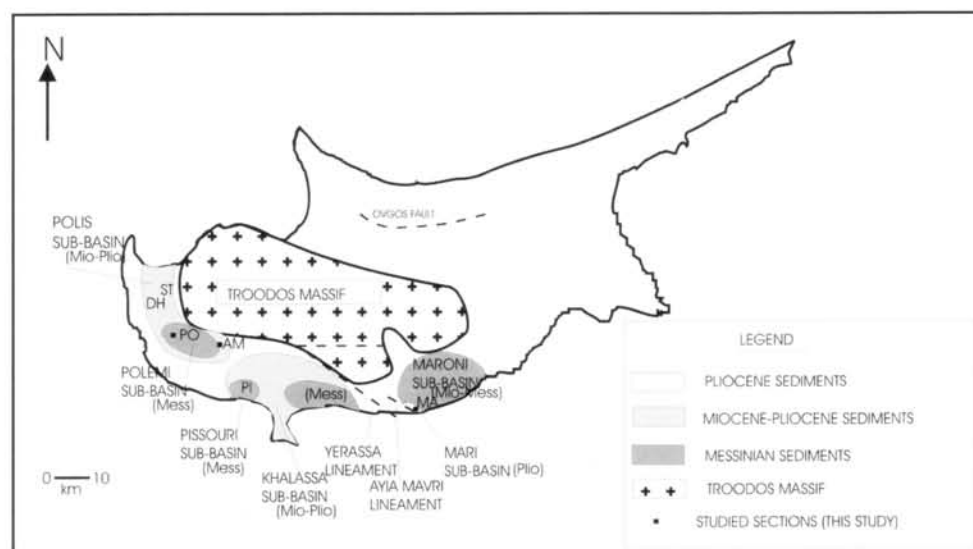
$$(\text{VarTD}) = \text{Lambda+} = [\sum_{i < j} (\omega_{ij} - \bar{\omega})^2] / [s(s-1)/2]$$

where $\bar{\omega}$ approximates the Delta+ value and s and ω_{ij} as above.

The lower the value of this index the more uniform is the distribution of species among the various taxonomic categories.

For both indices of Clarke and Warwick three hierarchical levels were here used: the species, the genus and the family, the latter converging to the superfamily Cytheroidea. The data were computed with the computer package PRIMER-5 (Plymouth Routines in Multivariate Ecologic Research) for Windows, version 5.2 (Clarke & Gorley, 2001).

Clarke and Warwick developed a randomisation



Text-fig. 1 - Geological map of Cyprus Island with the main depositional sub-basins (after Robertson *et al.*, 1991) and the location of the studied sections (AM - Amargeti, PO - Polemi, MA - Mari); dashed lines: major faults of south and west Cyprus.

test to detect differences in the average and/or the variation of taxonomic distinctness (review in Warwick & Clarke, 2001). A 95% probability funnel, using 5000 random selections from a "master list" allows to verify if the observed data of various samples significantly depart from sub-samples with an equivalent number of species extracted randomly from the master list. In our case we used the total taxonomical list of the nine sampling sections (153 species, cf. Tabs 3, 4).

Analysis of marine nematode fauna from "stressed" (anthropogenically polluted sediments) on the British coasts (Warwick & Clarke, 1998) showed lower values for the Delta+ index as compared for the values obtained from "normal" (unpolluted) benthic habitats. Data representative for "stressed" environments had values laying outside the 95% significance values of the simulated sub-samples. Therefore, the 95% significance line of the "funnel" represents a well-defined "objective" criterion when one intends to set the limits between normal and stressed ecological systems. We will use it here for the Cyprus ostracod data.

In order to better illustrate the meaning of the two taxonomic diversity indices we present below an example extracted from the sample Polemi 10358 (Text-fig. 5, Tabs 3, 4). This sample originating from the Athalassa Formation was dated as Pleistocene (Galoukas, 1995) and is represented by eight species belonging to six genera and five families. Four of the genera have one species while the others display two species. The probability that randomly extracted, two species will belong to different superspecific taxa is very high, hence the value of the Delta+ index is also high, i.e. over 90 units (Tab. 4). The value of the variation in taxonomic distinctness is low because the evenness of the five taxonomic lineages is high, i.e.

each family is represented by 1-2 genera and these ones by 1-2 species (Tabs 3, 4).

GEOLOGICAL BACKGROUND

The general geological structure of the island consists mainly of igneous rocks at the bottom, followed upwards by sedimentary formations of different composition and age.

The oldest geotectonically autochthonous part of Cyprus is the Troodos Massif (ophiolites) of Cretaceous age, Campanian or older (Text-fig. 1).

During early Tertiary times relatively thin (tens of metres) pelagic carbonates were deposited along the north margin of the Troodos ophiolite, while at the same time much thicker (>1000 m) successions were deposited in tectonically active basins in south Cyprus as the Maastrichtian-Miocene Lefkara Formation (Mantis, 1970; Robertson, 1976). In the Oligocene, during a time of relative tectonic quiescence, a gradual shallowing of the Troodos Massif took place (Upper Lefkara Formation) (Mantis, 1970; Robertson, 1977).

The Neogene evolution of Cyprus is marked by a fundamental change in sedimentation, from relatively uniform pelagic carbonate deposition (Upper Lefkara Formation), to much more varied carbonate and clastic sedimentation in tectonically controlled small basins bordering the Troodos ophiolite (Pakhna Formation) (Robertson, 1977). This early to late Miocene sedimentation took place throughout central and south Cyprus, south of the Ovgos fault, and probably also covered much of the Troodos ophiolite areas (Robertson, 1977).

On the top of the Pakhna Formation (Text-fig. 2) lie evaporitic lithofacies of the Messinian Kalavassos Formation (Eaton, 1987; Follows, 1990a). In the lower and upper parts of the Pakhna Formation, interstratified reefal units are exposed (Eaton, 1987; Follows & Robertson, 1990; Follows, 1990b), belonging to the Aquitanian-Burdigalian Terra Member and the Tortonian Koronia Member (Robertson *et al.*, 1991).

The Pliocene of Cyprus is represented by the Nicosia Formation (Text-figs. 3-5) which starts with locally exposed (e.g. Mari area) basal Pliocene silts unconformably overlying Miocene evaporites and marls (Robertson *et al.*, 1991), and continues with relatively stable deposition of marly sediments.

The Nicosia Formation is covered by bioclastic sediments of the Athalassa Formation, which is locally unconformably sitting on it. The Athalassa Formation is laterally equivalent to the Kakkaristra and Apalos Formations in south Cyprus (McCallum, 1989; McCallum & Robertson, 1990).

Later in the Pleistocene, all the circum-Troodos sedimentary basins are covered by coarse conglomerates, which overlie all older formations. Thus drastic updoming of the Troodos Massif took place during the Pleistocene (Robertson, 1977) which may reflect

		FORMATION	LITHOLOGY
PLEISTOCENE		ATHALASSA KAKKARISTRA APALOS	Conglomerates and Sandstones
PLIOCENE		NICOSIA	Marls, silts, muds, sandstone, conglomerate
MIOCENE	KALAVASSOS		Evaporites
	UPPER	KORONIA MEMBER	Reefal and bioclastic limestone
	MIDDLE	PAKHNA	Pelagic chalks, marls, calcarenites, conglomerates
	LOWER	TERRA MEMBER	Reefal and bioclastic limestone
OLIGOCENE		UPPER LEFKARA	Pelagic chalks and marls

Text-fig. 2 - Stratigraphic nomenclature of the Neogene of Cyprus (after Robertson *et al.*, 1991).

the initial underthrusting of thinned African continental margin crust, implying that little fully oceanic crust still persists in the East Mediterranean sea south of Cyprus (Dixon & Robertson, 1984). Radiometric dating of corals in coastal terrace deposits indicates that rapid uplift was over prior to Holocene times (Poole *et al.*, 1991), when the modern topography was attained. Cyprus is still a seismically active area.

BIO-LITHOLOGICAL DESCRIPTION OF THE SECTIONS AND SAMPLES

AMARGETI (A)

Amargeti is located in the southwest part of Cyprus (Text-fig. 1). The samples for this area were collected along a traverse which consists of a southwest-northeast trending section through the southeastern margin of the Polemi evaporite basin, near the southeastern termination of the Polis Graben.

The oldest geological unit in the area is the Lefkara Formation (Text-fig. 2) which comprises bioturbated foraminiferal chalk and whose age ranges from Late Cretaceous (Maastrichtian) to the Miocene (Robertson, 1977).

Following upwards, fossiliferous marls, chalks and thin (turbiditic) calcarenites can be found belonging to the Pakhna Formation. Hard micrites with *Discospirina* were found near the top of this unit, which is probably entirely of Mid to early Late Miocene age (Robertson, 1977).

The Pakhna Formation is overlain by more than 7 m of laminated, brecciated and massive gypsum, with hard laminated limestones and marls at the base, comprising together the Kalavassos Formation. According to Robertson (1977), these evaporites belong to the Late Miocene (Messinian).

The Kalavassos Formation is overlain by more than 3 m of marls containing large (up to 2 m) boulders of the Kalavassos gypsum in the lower part and the age of this unit assumed to be latest Miocene or early Pliocene.

The next unit upwards is the Nicosia Formation

with an unknown thickness (>10 m) of soft foraminiferal marls. The base of this unit in this area is thought to be of earliest Pliocene age (Robertson, 1977).

Overlying the Nicosia Formation are found locally gravels, sands, pebbly sandstones and sandy limestones which contain reworked microfossils and clasts of Troodos basic igneous rocks. These are assigned to the Quaternary, including also a small travertine deposit in the southwest of the area.

The three samples used here (Text-fig. 3) were dated and interpreted using Foraminifera and calcareous nannoplankton studied by Radley & Mondejar-Marchante (1990) (Tab. 1).

Sample 10351

Soft pale blocky to laminated foraminiferal marl (Nicosia-type) fills a small channel-like structure 1 m deep within massive weathered gypsum. A sample was collected from this marl.

Sample 10347

At this locality, a gypsum boulder bed is observed overlying the Kalavassos Formation. Northeast of this bed a marl sequence (with a sandy marl containing charophyte oogonia) including intraformational breccias was recorded and from this sandy marl a sample was taken.

Sample 10344

The section here contains 3 m of shelly bioturbated Nicosia-type marls (from which a sample was collected) with sandy lenses, overlain abruptly by approximately 3 m of irregularly bedded gravels (locally cemented), calcareous sandstones and clayey sands, with stringers of matrix-supported clasts.

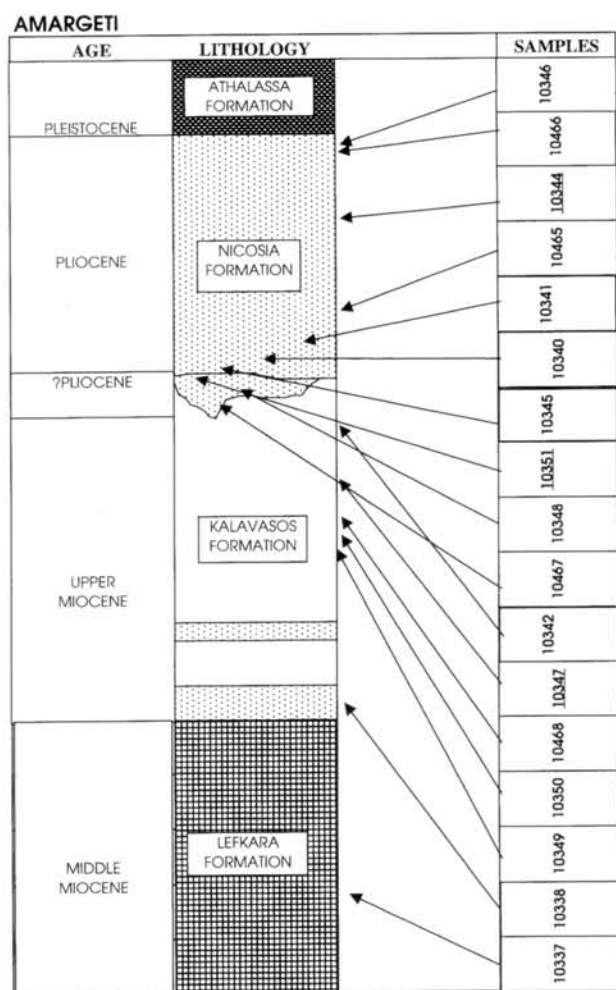
POLEMI (P)

The studied area is around the village of Polemi, which is located in the SW part of the island and about 15 km NE of Paphos. Geologically, the area is placed in the Polis Basin (Text-fig. 1).

In general, the sequence consists of Messinian evaporitic deposits (Kalavassos Formation), occupying the Polemi Basin (Robertson, 1977) and overlain by Pliocene marls (Nicosia Formation), with coarse

SAMPLE	NANNOFOSSIL ZONE	FORAMS ZONE	AGE	ENVIRONMENT
10351	?	<i>G. margaritae</i>	Early Pliocene	open marine
10347	Late Miocene – Early Pliocene	?	Late Miocene – Early Pliocene	restricted marine (?freshwater influence)
10344	?	Late Miocene – Late Pliocene	Earliest Pliocene	outer shelf to bathyal marine
10341	No markers (reworked ?)	No markers (reworked ?)	lateral equivalent of the gypsum boulder bed	(shallow?) marine

Tab. 1 - Chronostratigraphic data for the Amargeti samples based on Foraminifera and calcareous nannoplankton (after Radley & Mondejar-Marchante, 1990).



Text-fig. 3 - Stratigraphy of the Amargeti section, including the number of the sample units (from Galoukas, 1995).

bioclastic limestones of the Athalassa Formation on the top (Text-fig. 4). The four samples used here (Text-fig. 4) were dated and interpreted using Foraminifera and calcareous nannoplankton (Tab. 2) studied by Outram & McCarthy (1990).

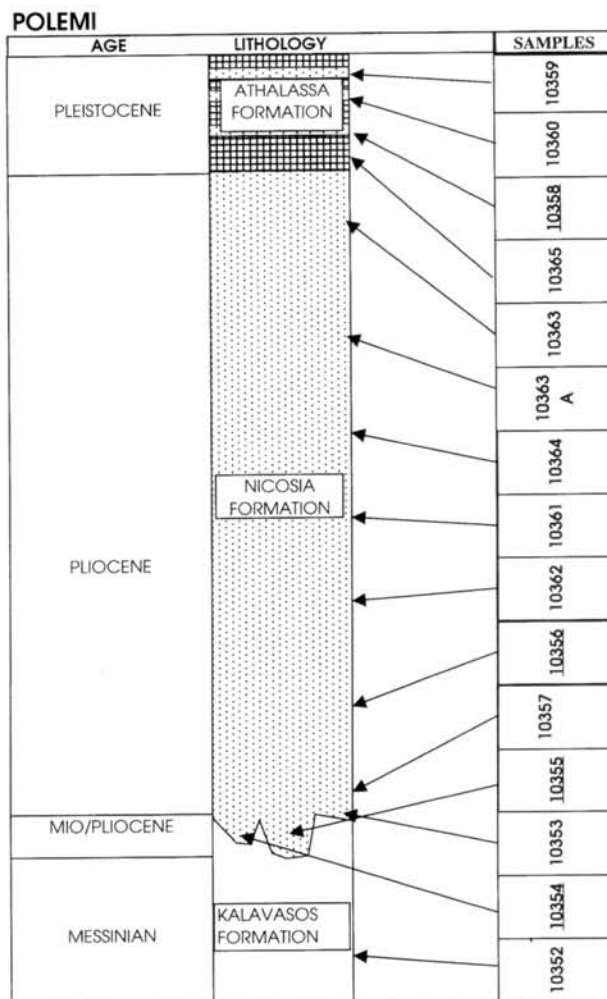
Sample 10354

A marly gypsum bed between two gypsum beds. The marl was white, soft and fine-grained and was sampled in the belief that it is the top of the Kalavasos Formation.

Sample 10355

This is a sample taken from a fine-grained creamy white marl at the same height as sample 10354 but further to NE. This sample was taken for correlation of the two samples and (due to its position at the base of a faulted block that was capped by Nicosia and Athalassa Formations) in an attempt to find out whether this marl was at the base of the Nicosia or the top of the Kalavasos Formation.

Sample 10356



Text-fig. 4 - Stratigraphy of the Polemi section, including the number of the sample units (from Galoukas, 1995).

Green/buff fine-grained marl that weathers grey.

Sample 10358

Buff, coarse grained bioclastic limestone with corals, oysters and *Pecten* present.

MARI (M)

The Mari section is located between the coast and the main road from Limassol to Nicosia on the south coast of Cyprus (Text-fig. 1). It may be considered representative of those sediments that have been deposited in local, tectonically controlled, subsiding basins that adjoined shallow areas of small islands with fringing lagoons, reefs and shoals.

The Mari section (Text-fig. 5) consists of approximately 35 m of homogeneous, in parts heavily bioturbated, green-grey clays, grey-brown silts and sands, overlain by approximately 15 m thickness of conglomerates, aeolian dune sands and thin-bedded silts. In the fine-grained sections, the transition from

SAMPLE	NANNOFOSSIL ZONE	FORAMS ZONE	AGE	ENVIRONMENT
10358	Poor	N9-Recent	Middle Miocene – Recent	Inner shelf (high salinity ?)
10356	Late Miocene	N16-N21	Late Miocene – Late Pliocene	Continental shelf / Outer slope
10355	Sparse microfossils	N19-N21	Pliocene	Continental slope
10354	Poor	No Forams	Middle Miocene – Recent	Brackish, Estuarine

Tab. 2 - Chronostratigraphic data for the Polemi samples based on Foraminifera and calcareous nannoplankton (after Outram & McCarthy, 1990).

the clay to the silt was noticed to be gradual in places, except from the upper silt which overlies the silty clay with an irregular boundary.

The whole sequence is dominated by both intact and broken shells of bivalves and gastropods. Vertical burrows containing wood remains and laminae of organic material are shown in the brown clay band. These horizons seem to be strongly affected by diagenetic processes (responsible for the formation of layers and lenses of iron oxides, which eventually destroyed the ostracod fauna in places). Also, the orange, fine-grained sand horizon, which is placed between the two irregular boundaries, just below the conglomerates, is laminated, slightly bioturbated and less affected by diagenesis, containing fragmented and intact shells of bivalves, gastropods and scaphopods.

The age of the Mari sequence is supposed to be Early Pliocene (Pavlakelli, 1986). Three samples, 9428, 9429 and 9431, (Text-fig. 5) are examined from the section. The generally low density of the ostracods limits the value of the results to the specific basin only. The environment interpreted for the lower parts of the section (where the above samples belong) is a deep, open marine environment with an autochthonous fauna. More specifically, the bottom of this faulted basin is believed to correspond to continental slope depth (lower part of the Mari sequence), with a temperature higher than 10°C (thermosphaeric basin, i.e. depth <500 m). The section has not been studied for planktonic foraminifera and calcareous nannoplankton.

RESULTS FROM THE "TRADITIONAL" STUDY OF SAMPLES

AMARGETI (Text-fig. 3)

The distribution of the cytheroid ostracods of the three samples (10347, 10351, and 10344) is presented in Tab. 3 and additionally data are presented in Galoukas (1995). In these samples, ostracods were associated with variable ratios of calcareous nannofossils, benthic and/or planktonic Foraminifera, accompanied in some cases with fragments of other fossils like echinoid spines (samples 10351 and 10347) and charophytes (sample 10347). *Cyprideis torosa* Jones

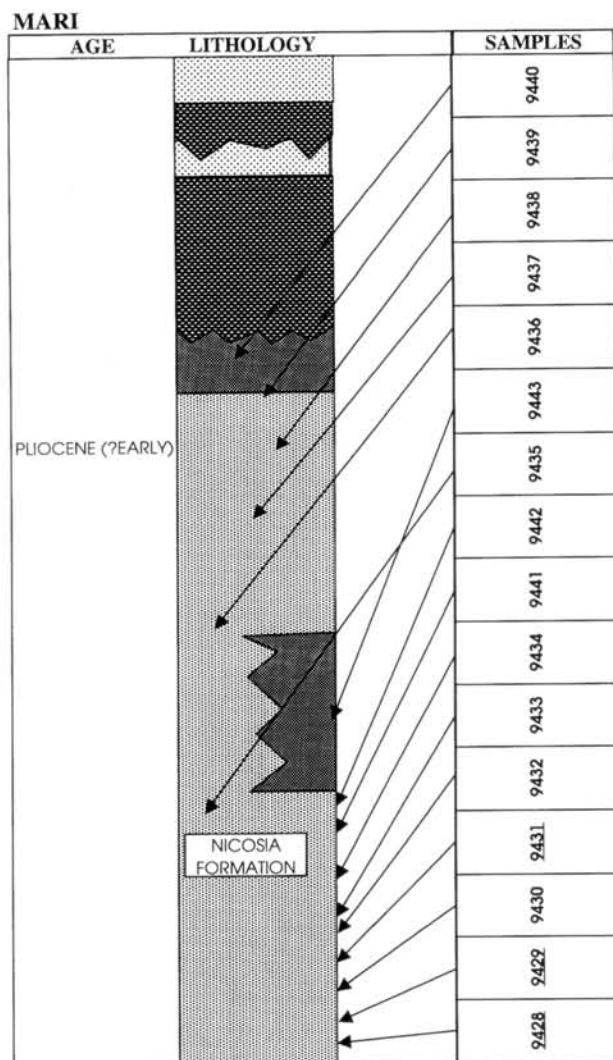
dominates sample 10347 representing 86.5% of the specimens. There are only four non-cytheroid species belonging to the genera *Polycope*, *Cytherella*, and *Bythocypris*. So, the most probable depositional environment for this sample would be a brackish one with moderate marine influence.

Next, in sample 10351 brackish conditions with marine influence are shown by the important numbers of *Cyprideis* valves (indicating brackish conditions) accompanied by *Loxococoncha*, *Callistocythere*, *Monoceratina*, *Xestoleberis*. Only two carapaces of a non-cytheroid (*Argilloecia acuminata* Mueller) were sampled. Then, a deep marine environment is established (Galoukas, 1995), which is gradually transformed into an environment (sample 10344) with almost psychrosphaeric conditions (*Oblitocythereis mediterranea* Benson, *Henryhowella asperima* Reuss). Not a single valve of the characteristic psychrosphaeric ostracod species *Agrenocythere pliocenica* Seguenza was found. Beside Cytheroidea taxa there are 11 non-cytheroids belonging to the genera *Cytherella*, *Bythocypris*, *Argilloecia*, *Pontocypris*, *Paracypris*, and *Pontocyprilla*.

POLEMI (Text-fig. 4)

In the four samples (10354, 10355, 10356, and 10358) examined, calcareous nannofossils occur. With the exception of sample 10354, benthic and planktonic Foraminifera have been reported as co-occurring with the other microfossils.

As can be seen from Tab. 3, there are (with the exception of 10354 and 10355) very few common ostracods in any two adjacent samples. This fact clearly indicates the vertical development of different environments through the section. The less species two adjacent samples have in common, the more likely these samples represent different environments. Using this principle, one environment should be accepted for sample 10354, which is then slightly differentiated in sample 10355 with the development of a population consisting of many of the species appearing in 10354 plus some new species. The major components of these samples are species of *Leptocythere*, *Cyprideis*, *Tyrrhenocythere*, *Loxocauda*, and *Loxococoncha*. Additionally, Candoninae species were noted (Galoukas, 1995). Outram & McCarthy (1990) gave in their study based



Text-fig. 5 - Stratigraphy of the Mari section, including the number of the sample units (from Galoukas, 1995).

on Foraminifera, a "crisis" environment for sample 10354 of uncertain age and an open ocean continental slope environment (with more inner shelf influences) for sample 10355 of Zanclean-Early Piacenzian (N19-N21) age. Since they did not give any further explanation of the sort of "crisis" it is taken here that they meant non-marine conditions for sample 10354, which is supported by the ostracods. Further, for sample 10355 ostracods give a much shallower environment (littoral) with brackish conditions and freshwater (continental) influences. These freshwater signs may very well be the remains of an earlier or adjacent continental environment (sample 10354). The option of an adjacent continental environment is adopted here since sample 10355 was collected from the same level as 10354 but further to north-east. This means that two types of ecosystems existed at the same time but in different locations, i.e. one ecosystem rich in *Euxinocythere* (sample 10354) in one place, and an-

other with *Tyrrhenocythere*, *Leptocythere* (*Amnicythere*), *Pontoleberis* further north-east (sample 10355). Additionally in sample 10354 a diverse subassemblage of Candoninae belonging to *Pontoniella* and *Camptocyprina* were identified (Galoukas, 1995). *Loxoconcha* (*Loxocorniculina*) *djaffarovi* Schneider as well as various other *Loxoconcha* species and *Cyprideis torosa* Jones were living in both ecosystems.

The genus *Tyrrhenocythere* first appears in sample 10355 with a large number of valves (Tab. 3). Sissingh (1982) suggested *Tyrrhenocythere* as an immigrant when he found it in an assemblage which is very similar to the one of the present study, but its quantity here is far higher (showing also a good balance between left/right valves) and therefore it should be indigenous to that environment, together with *Loxoconcha djaffarovi* Schneider and *Leptocythere* (*Amnicythere*) *litica* Livental. The favourite environment of the latter is a stenohaline one (salinity about 12-13‰) with a temperature of 15.5-16°C (Carbonnel, 1978). From the present data it is inferred that the two ecosystems were two warm, saline "lakes" with that of 10354 being less saline as suggested also by the presence of the rich fauna of candonids (Galoukas, 1995).

The existence of planktonic Foraminifera in sample 10355 (Outram & McCarthy, 1990) may reflect either: (1) that the ecosystem of this sample was a lagoon connected with the open sea, or (2) that it was a lake but something rapid happened, (e.g. eustatic rise of the sea-level, or tectonic activity) and there was temporary influx of open-marine water. If this happened, the rise of sea-level did not have any influence in sample 10354 probably because it was situated as at the present day higher than the level of the sample 10355. Also, the fact that no Pontian ostracods have been recovered from off-shore samples DSDP west of Cyprus (Benson, 1972a; Carbonnel, 1978) probably indicates that the sampling area was completely dried-up at that time, which means that the Polemi "lakes" were closed to the west (where the DSDP cores were collected). Concerning the ages of these two samples, their species composition indicates (Tabs 2, 3) a Pontian age for both samples.

Going further up in the Polemi section, the ostracod fauna indicates a thermosphaeric environment (Galoukas, 1995) while a little later, in sample 10356, a sudden strong appearance of fully marine (psychrosphaeric) species is shown; they are thought to be of Pliocene age. A diverse non-cytheroid fauna with various *Argilloecia*, *Paracypris*, *Bythocypris*, *Macrocypris*, *Cytherella*, and *Polycopse* taxa were identified (Galoukas, 1995). This association has many similarities with both the assemblages of the same age from neighbouring areas Steni and Dhrymou (Galoukas, 1995) and the assemblages that have been recovered from an off-shore DSDP core (Benson, 1972a).

One of the abundant species, e.g. in the sample 10356 (Tab. 3) is *Agrenocythere pliocenica* Seguenza, indicative of psychrosphaeric conditions (i.e. At-

lantic cold, dense bottom-waters with temperatures $<8-10^{\circ}\text{C}$). The sudden faunal transition from warm non-marine ($15.5-16^{\circ}\text{C}$) to deep cold marine ($<8-10^{\circ}\text{C}$) species at the beginning of the Pliocene, shows a rapid change in the environment of the Levantine Basin which is in full accordance with what happened in the Western Mediterranean basins (the Balearic and the Tyrrhenian B.) at the same time (Benson, 1972b). This transition happened possibly as a result of an influx of oceanic waters (with the opening of Gibraltar), which filled up the pre-existing Messinian "lakes" and re-established the marine communication between the Polemi area and the sites of the off-shore drilling west of Cyprus, allowing development of a uniform cold, deep-water ostracod community.

MARI (Text-fig. 5)

The three samples examined (9428, 9429, and 9431) contain more or less equal numbers of left/right ostracod valves, which are very uniformly distributed, and few carapaces (Tab. 3). In general, in this section there is an almost uniform distribution of the ostracods in the samples indicating probably relatively stable conditions through the time when the sampled sequence was deposited.

The association of *Graptocythere hscripta* Capeder, *Aurila convexa* Baird and *Loxoconcha ovulata* Costa forms a very distinct group throughout the whole section. *Aurila* and *Loxoconcha* are known to inhabit shallow marine environments while *Graptocythere* deeper ones. Additionally valves of *Cytherella*, (e.g. *C. terquemi* Sissingh) were also present (Galoukas, 1995). A possible explanation for this phenomenon is the transportation of the shallow water species into deeper water either by currents or by tectonic disturbance. The quantitative distribution of the valves (Tab. 3) and the right/left valve balance of the shallow water species are indicative of the autochthonous nature of the shallow water species, rather than of the deep-water assemblage. We suggest therefore (at least for the samples 9428 and 9429) the existence of outer neritic conditions.

In later samples (Galoukas, 1995) the presence of additional deep-water species is observed, indicating as an assemblage a depth of approximately 500 m but not psychrosphaeric due to the absence of clearly psychrosphaeric species like *Agrenocythere pliocenica* Seguenza.

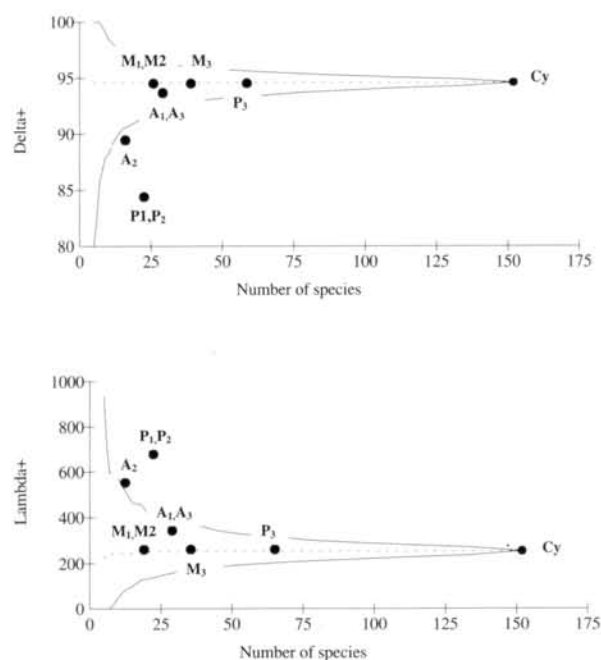
The palaeogeographic setting for the Mari section as concluded from the above information, fits with that proposed by Pavlakelli (1986) according to which the region was a small faulted basin during the Pliocene, with shallow calcareous platforms immediately adjacent to it (including samples 9428 and 9429). An eastward shallowing of the Mari Basin in the Pliocene, followed by erosion is also suggested by McCallum (1989).

RESULTS USING THE "TAXONOMIC DIVERSITY" APPROACH OF CLARKE AND WARWICK

Tab. 4 and Text-fig. 6 present information on the taxonomic diversity of the samples from the Amargeti, Polemi and Mari section. With the exception of the data for the sample Polemi-10358 (P4), which was used in the previous section for the demonstration of the way the Clarke and Warwick's algorithm work, the other nine data sets will be here described.

AMARGETI

The cytheroid species richness varies between 27 species in the samples 10347 and 10344 (A1 and A3) and 11 species in the sample 10351 (A2). In this latter sample the number of genera, both the $G_{1/2}$ and G_3 ones, and the number of families is markedly lower than in the former two samples. The value of the average taxonomic distinctness (the Delta+ index) for the A1 and A3 is higher than those of the A2 sample. An opposite trend is visible for the values of the variation of taxonomic distinctness (the Lambda+ index), i.e. the A2 has a much higher value than those of the other two samples (Tab. 4). The values of the both indices for A2 lay outside the 95% probability funnel



Text-fig. 6 - Taxonomic diversity of the Neogene Cytheroidea from Amargeti (A), Polemi (P) and Mari (M) sections; upper panel - The average taxonomic distinctness (Delta+) for the various samples; Cy - Total species list; lower panel - Variation in taxonomic distinctness (Lambda+); dashed line - the simulated mean, thin line - 95% probability funnel for the expected range of Delta+ respectively Lambda+ values; assemblage code as in Tab. 4 (A1, A2, A3, P1, P2, P3, M1, M2, M3, Cy).

Nr.	TAXA	Amargeti					Mari					Polemi				
		10347	10351	10344	9428	9429	9431	10354	10355	10356	10358					
		C	RV	LV	C	RV	LV	C	RV	LV	C	RV	LV	C	RV	LV
A	LOXOCOCHIDAE:															
A1	<u>Loxocauda</u>															
1	<i>Loxocauda cf. stevanovici</i>											12	8	1		
2	<i>Loxocauda azeri</i>													1		
3	<i>Loxocauda decipiens</i>															
4	<i>Loxocauda limata</i>											1	2	1	1	
5	<i>Loxocauda stevanovici</i>											1	1	1		
A2	<u>Loxoconcha</u>															
6	<i>Loxoconcha cumsacui</i>											1	2			
7	<i>Loxoconcha djaffarovi</i>											19	25	73	43	35
8	<i>Loxoconcha affinis</i>								1						6	9
9	<i>Loxoconcha alata</i>									1		2	1			1
10	<i>Loxoconcha cf. kalickyi</i>		2													
11	<i>Loxoconcha moncharmonti</i>			3												
12	<i>Loxoconcha ovulata</i>									4	3					
13	<i>Loxoconcha petasus</i>	1	3	3					1			4	1	2		
14	<i>Loxoconcha petkovici</i>									4	1	3	6		6	2
15	<i>Loxoconcha schweyeri</i>													5	1	9
16	<i>Loxoconcha sp. 4</i>													4	1	2
17	<i>Loxoconcha sp. 5</i>								1					5	2	2
18	<i>Loxoconcha sp. 7</i>													1	2	7
19	<i>Loxoconcha sp. 8</i>	2	3	2	1	1										
20	<i>Loxoconcha sp. 9</i>		1													
21	<i>Loxoconcha sp. 10</i>			2										1	2	3
22	<i>Loxoconcha sp. 11</i>			1												
23	<i>Loxoconcha sp. 12</i>															
24	<i>Loxoconcha sp. 14</i>															
25	<i>Loxoconcha turbida</i>									1	1		1			
B	CYTHEROIDEAE:															
B1	<u>Aversoalva</u>															
26	<i>Aversoalva lancei</i>															
B2	<u>Hemicytherura</u>															
27	<i>Hemicytherura hellenica</i>		3	2	1					1					2	
28	<i>Hemicytherura videns</i>															7
B3	<u>Cytheropteron</u>															
29	<i>Cytheropteron aemulum</i>															
30	<i>Cytheropteron boldi</i>															

Tab. 3 - Qualitative and quantitative data of Cytheroidea ostracods used for the study of the taxonomic diversity of Amargeti, Polemi and Mari samples (from Galoukas, 1995).

Nr.	TAXA	Amargeti						Mari						Polemi					
		10347		10351		10344		9428		9429		9431		10354		10355		10356	
		C	RV	LV	C	RV	LV	C	RV	LV	C	RV	LV	C	RV	LV	C	RV	LV
31	<i>Cytheropteron cronini</i>																		
32	<i>Cytheropteron latum</i>																		
33	<i>Cytheropteron monoceros</i>																		
B4	<i>Eucytherura</i>																		
34	<i>Eucytherura complexa</i>							1											
35	<i>Eucytherura gibbera</i>																		
36	<i>Eucytherura mistretai</i>							1											
37	<i>Eucytherura sp.</i>							1											
B5	<i>Kangarina</i>																		
38	<i>Kangarina abyssicola</i>							1											
B6	<i>Pedicythere</i>																		
39	<i>Pedicythere mirabilis</i>																		
40	<i>Pedicythere sp.</i>																		
B7	<i>Pseudocytherura</i>																		
41	<i>Pseudocytherura calcarata</i>							2	2										
B8	<i>Semicytherura</i>																		
42	<i>Semicytherura acuminata</i>																		
43	<i>Semicytherura acuticostata</i>							1				1							
44	<i>Semicytherura cf. punctata</i>																		
45	<i>Semicytherura dispar</i>								1				2						
46	<i>Semicytherura incongruens</i>																		
47	<i>Semicytherura rara</i>												1						
48	<i>Semicytherura sp. 1</i>																		
C	TRACHYLEBERIDIDAE:																		
C1	<i>Agrenocythere</i>																		
49	<i>Agrenocythere pliocenica</i>																		
C2	<i>Bosquetina</i>																		
50	<i>Bosquetina sp. 2</i>											1							
C3	<i>Buntonia</i>																		
51	<i>Buntonia sublatissima</i>							1											
52	<i>Buntonia sequenziana</i>																		
53	<i>Buntonia miranda</i>																		
54	<i>Buntonia textilis</i>											1	1	1					

		10347			Amargeti					Mari					Polemi																						
		C	RV	LV	10351	C	RV	LV	10344	C	RV	LV	9428	C	RV	LV	9429	C	RV	LV	9431	C	RV	LV	10354	C	RV	LV	10355	C	RV	LV	10356	C	RV	LV	10358
Nr.	TAXA																																				
77	<i>Krithe</i> sp. 5											2									1	2															
D2	<u>Parakrithe</u>																																				
78	<i>Parakrithe dactylomorpha</i>		1																																		
79	<i>Parakrithe dimorpha</i>								1																												
80	<i>Parakrithe</i> sp. 2																																				
E	<u>LEPTOCYTHERIDAE:</u>																																				
E1	<u>Callistocythere</u>																																				
81	<i>Callistocythere gilva</i>							1																													
82	<i>Callistocythere macilenta</i>		3	1																															2	1	1
83	<i>Callistocythere montana</i>							1									1		3	1															1		
84	<i>Callistocythere</i> sp.1		1																																		
85	<i>Callistocythere</i> sp. 2																																				
86	<i>Callistocythere</i> sp. 3											1																									
87	<i>Callistocythere</i> sp. 5																																			1	5
E2	<u>Ionicythere</u>																																				
88	<i>Ionicythere golnarae</i>																2																				
E3	<u>Leptocythere</u>																																				
89	<i>Leptocythere affinis</i>																																				1
90	<i>Leptocythere litica</i>																																				
91	<i>Leptocythere sinegubi</i>																																				
92	<i>Leptocythere stanchevae</i>																																				
93	<i>Leptocythere bisaltiana</i>																																				
94	<i>Leptocythere quinquetuberculata</i>																																				
95	<i>Leptocythere schweyeri</i>																																				
96	<i>Leptocythere cf. caspia</i>																																				
97	<i>Leptocythere cf. nostrata</i>																																				
98	<i>Leptocythere cymbula</i>																																				
99	<i>Leptocythere microlata</i>																																				
100	<i>Leptocythere multituberculata</i>																																				
101	<i>Leptocythere</i> sp. 1																																				
102	<i>Leptocythere</i> sp.3																																				
103	<i>Leptocythere</i> sp. 4		1																																		

Nr.	TAXA	Amargeti			Mari			Polemi		
		10347	10351	10344	9428	9429	9431	10354	10355	10358
		C RV LV	C RV LV	C RV LV	C RV LV	C RV LV	C RV LV	C RV LV	C RV LV	C RV LV
F	XESTOLEBERIDAE:									
F1	Xestoleberis									
104	<i>Xestoleberis attilata</i>									
105	<i>Xestoleberis communis</i>	1		1			4	1	1	5
106	<i>Xestoleberis decipiens</i>	1	2							2
107	<i>Xestoleberis dispar</i>	2	1	1						3
108	<i>Xestoleberis margaritea</i>	1	4			1	2			9
109	<i>Xestoleberis sp.1</i>							1	1	1
110	<i>Xestoleberis sp.2</i>									
111	<i>Xestoleberis ventricosa</i>			1	1	2		2	2	
G	CYTHERIDAE:									
G1	Cytheromorpha									
112	<i>Cytheromorpha fuscata</i>		1							
G2	Kroemmelbeinella									
113	<i>Kroemmelbeinella coae</i>				1	1				1
G3	Paijenborchella									
114	<i>Paijenborchella tocosa</i>									
H	HEMICYTHERIDAE:									
H1	Aurila									
115	<i>Aurila aspidoides</i>									21
116	<i>Aurila convexa</i>				6	8	5	6		11
117	<i>Aurila cruciata</i>									1
118	<i>Aurila flalodes</i>	1								
119	<i>Aurila maculosa</i>									
120	<i>Aurila pigadiana</i>	1	2		2					3
121	<i>Aurila preacuta</i>									1
122	<i>Aurila punctata</i>	1								3
123	<i>Aurila speyeri</i>									
124	<i>Aurila ulicznyi</i>	3						1		1
125	<i>Aurila vena</i>									1
H2	Caudites									
126	<i>Caudites calceolatus</i>				1		1	2		1
H3	Graptocythere									
127	<i>Graptocythere hscripta</i>				1	2	1			2

Nr.	TAXA	Amargeti			Mari			Polemi				
		10347	10351	10344	9428	9429	9431	10354	10355	10356	10358	
		C RV LV	C RV LV C	RV LV C	C RV LV C	C RV LV C	C RV LV C	C RV LV C	RV LV C	RV LV C	RV LV C	
H4	<i>Hemicytheria</i>											
128	<i>Hemicytheria</i> sp.	1										
H5	<i>Mutilus</i>											
129	<i>Mutilus retiformis</i>											1
H6	<i>Pachycaudites</i>											
130	<i>Pachycaudites ungeri</i>			1						1		
H7	<i>Pokorniyella</i>											
131	<i>Pokorniyella deformis</i>	2										
H8	<i>Quadracythere</i>											
132	<i>Quadracythere prava</i>						4 3			1 1		
H9	<i>Tyrrenocythere</i>											
133	<i>Tyrrenocythere filipes</i>	1 1 3										
134	<i>Tyrrenocythere pannonicum</i>								1 22 27			
135	<i>Tyrrenocythere pignatii</i>	1										
136	<i>Tyrrenocythere</i> sp. 1	1 1										
137	<i>Tyrrenocythere</i> sp. 3		1									
H10	<i>Urocythereis</i>											
138	<i>Urocythereis distinguenda</i>						2 2			6 4		
I	BYTHOCYTHERIDAE:											
I1	<i>Monoceratina</i>											
139	<i>Monoceratina mediterranea</i>		1							1		
140	<i>Monoceratina</i> sp.					1						
I2	<i>Pseudocythere</i>											
141	<i>Pseudocythere caudata</i>									1 2		
I3	<i>Profundocythere</i>											
142	<i>Profundocythere splendida</i>			1								
J	NEOCYTHERIDAE:											
J1	<i>Pseudopsammocythere</i>											
143	<i>Pseudopsammocythere similis</i>					1				1		
144	<i>Pseudopsammocythere kollmanni</i>					1 2	1 1			5		4

Tab. 3 - continued

Nr.	TAXA	Amargeti			Mari			Polemi					
		10347	10351	10344	9428	9429	9431	10354	10355	10356	10358		
		C RV LV	C RV LV C	RV LV C	RV LV C	RV LV C	RV LV C	RV LV C	RV LV C	RV LV C	RV LV C	RV LV	RV LV
K	PARADOXOSTOMATIDAE:												
K1	<i>Paracytheroideis</i>												
145	<i>Paracytheroideis mediterranea</i>											1	
K2	<i>Schlerochilus</i>												
146	<i>Schlerochilus</i> sp.								1				
L	PARACYTHERIDEIDAE:												
L1	<i>Paracytheridea</i>												
147	<i>Paracytheridea depressa</i>											1	
148	<i>Paracytheridea insculta</i>											3	
149	<i>Paracytheridea</i> sp.						1						
M	CYTHERIDEIDAE:												
M1	<i>Cytherissa</i>												
150	<i>Cytherissa bogatschovi</i>								1				
M2	<i>Cyprideis</i>												
151	<i>Cyprideis torosa</i>	34	260	215	64	77	72					1	
152	<i>Cyprideis triangularis</i>	1						1	19	11	14	16	
M3	<i>Neocyprideis</i>												
153	<i>Neocyprideis pseudodonta</i>	1											
N	CUSHMANIDEIDAE:												
N1	<i>Cushmanidea</i>												
154	<i>Cushmanidea elongata</i>						1						

Tab. 3 - continued

for the expected range, while the A1 and A2 values lay closely to the simulated mean value (Text-fig. 6).

POLEMI

The taxonomic diversities of the samples 10354 and 10355 are very similar. There are more or less the same number of species as well as of $G_{1/2}$ and G_3 genera and families. The Delta+ and the Lambda+ indices show similar trends as in the case of Amargeti A2 sample, i.e. the average taxonomic distinctness is lower than 90 units and the variation of taxonomic distinctness is over 600 units. The sample 10356 (P3) displays a markedly high species richness (65) as compared to the other samples (Tab. 4), a notoriously high number of genera with 1-2 species and a high number of families (13). The value of the Delta+ index lay above 90 units and those of the Lambda+ below 250. The P1 and P2 values lay outside the 95% probability funnel for the expected range (Text-fig. 6).

MARI

The three samples 9428, 9429 and 9431 display high Delta+ and low Lambda+ values, i.e. around 95 units for the former index and below 250 units for the latter one (Tab. 4). The species richness varies between 22 and 33, the total number of genera between 15 and 22 and the number of families between 8 and 10. All the values of the two taxonomic indices for the Mari section here used lay within the 95% probability funnel for the expected range of their diversity (Text-fig. 6).

Summing up there are three samples (A2, P1, P2) which display values below 90 units for the average taxonomic distinctness and high values (above 600) for the variation of taxonomic distinctness. They contrast with the other six samples here analysed, which show an opposite trend. The significance of these data will be evaluated in the next section.

DISCUSSION AND CONCLUSIONS

From the interpretation of the ostracod assemblages of the sections presented above, it is concluded that the environment (and consequently the palaeogeography) was not synchronous changing with time at different places along the west, southwest, and south Cyprus.

A composite palaeoecological history for all the sections together (and consequently for the west and south of Cyprus) would start from the Messinian with alternations of limnic (lacustrine) and brackish water conditions up to the earliest stages of the Pliocene. In the Polemi region, the section starts later in the Messinian with limnic conditions, which became brackish just before the Pliocene.

The beginning of the Pliocene finds the Mari area with inner neritic conditions, while at the same time

brackish conditions dominate the Polemi and Amargeti areas. A little later, in Early Zanclean, marine thermosphaeric conditions dominate the sections and progressively towards the mid Pliocene, a deepening of all the sections is observed. This, in the areas of Amargeti and Mari has to be the result of local tectonic activity since no occurrence of clearly psychrosphaeric species has been noticed.

Traditional micropalaeontological analysis showed for Amargeti A2, Polemi P1 and Polemi P2 a strong departure from eumarine conditions (this latter commonly characterised by a high biological diversity). The ostracod data reanalysed with the probabilistic approach of Clarke and Warwick give for the taxonomic diversity congruent results with the conclusions derived from a traditional micropalaeontological analysis. The three samples mentioned above, laying outside the 95% confidence limits of the simulated probable diversity, point out to a "crisis" experienced by the cytheroid taxocenosis.

The analysis of the ostracod data of Cyprus using the taxonomic diversity algorithm has the merits to allow a rapid comparison in a synthetic way of abundant taxonomic data. It complements well the traditional micropalaeontological analysis and stimulates further examination of the palaeobiological and/or palaeoecological meaning of the information encapsulated in the ostracod assemblages. In this way the taxonomic diversity approach used here forms a kind of epistemological "smoking gun" (for this latter concept see Cleland, 2001), i.e. it stimulated our interest to re-examine the data set of Tab. 3.

The Polemi P3 is remarkable through the high diversity suggesting also a high heterogeneity of the environment *sensu* Thienemann's first biocenotic rule (Thienemann, 1954). It confirms Gaston & Williams (1996) view, which consider that the taxonomic diversity in the marine benthic realm peaks at intermediate depths. The other samples present lower dominance of supraspecific taxa, e.g. at Amargeti A1 and A3 loxoconchids represents less than 20% of taxa and there is an important contribution of the Cytheruridae, Hemicytheridae, Trachyleberididae, Krithidae and Xestoleberididae to the given assemblages (Tab. 3). A similar trend can be observed also in the three Mari samples.

If G. (Kino) Bonaduce would examine the Mari M1-M3 and the Polemi P3 samples, he would tell us that the taxonomic diversity is much similar with what he saw in the samples from the Gulf of Naples (Puri *et al.*, 1964) or in those of the Adriatic Sea (Bonaduce *et al.*, 1975). They point out to conditions with a palaeobathymetry of more than 100 m deep, an inference which came out also from the traditional palaeontological investigation of Galoukas (1995).

The cytheroid taxocenosis of Amargeti A2 and the Polemi P1 and P2 are dominated by species of two ostracod lineages, the Loxoconchidae and the Leptocytheridae, generally characteristic for shallow

Code	Site & Sample No.	Formation	Age	Species Richness (No.)	Genus $G_{1/2}$ (No.)	Genus G_3 (No.)	Fam. (No.)	AvTD	VarTD
A1	Amargeti-10347	Kalavassos F.	U. Miocene	27	10	4	9	92.69	335.9
A2	Amargeti-10351	B-Nicosia F.	Pliocene ?	12	7	1	7	89.39	577.7
A3	Amargeti-10344	Nicosia F.	Pliocene	27	14	3	9	92.69	329.6
P1	Polemi-10354	B-Nicosia F.	Mio/Pliocene	22	5	3	5	84.42	661.4
P2	Polemi-10355	B-Nicosia F.	Mio/Pliocene	21	5	3	6	84.44	668.1
P3	Polemi-10356	Nicosia F.	Pliocene	65	25	7	13	94.49	234.6
P4	Polemi-10358	Athalassa F.	Pleistocene	8	6	0	5	92.86	345.8
M1	Mari-9428	Nicosia F.	Pliocene	23	16	1	8	94.73	226.9
M2	Mari-9429	Nicosia F.	Pliocene	22	13	2	8	94.95	258.3
M3	Mari-9431	Nicosia F.	Pliocene	33	18	4	10	95.01	212.9
Cy	Master species list (A, P, M / 1-3)	Kalavassos & Nicosia F.	Miocene & Pliocene	153	37	14	14	94.56	257.3

Tab. 4. - Taxonomic diversity of Cytheroidea assemblages of Cyprus; $G_{1/2}$ – genus with 1 or 2 species; G_3 – genus with 3 or more species; AvTD – Average Taxonomic Distinctness; VarTD – Variation in Taxonomic Distinctness (additional explanations in text); B – basis, F – formation.

waters of marginal marine habitats, e.g. open lagoons and/or peri-coastal lakes. More than 50% of species in these samples belong to genera of these two families. These data fit the second biocenotic rule of Thienemann (1954) pointing out to stressful and/or strongly disturbed environments. From the inspection of Tab. 3 one notices that each of the three samples reflecting “stressful” environments is characterised also by a lower number of genera within their respective families, as compared to the “normal” eumarine assemblages. So combining the values of the taxonomic diversity indices of Clarke and Warwick with a careful examination of the ecological preferences of the various ostracode taxa here presented one can note that at each level of the Linnean hierarchy (species, genus and family) there is biological information which can be used for palaeoenvironmental reconstruction.

We conclude this discussion pointing out that the Clarke and Warwick's taxonomic diversity indices are useful descriptors for past environmental changes and should be more widely used in palaeontology in conjunction with other traditional approaches.

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