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Paleoecology of a Pliocene coral reef in Cyprus: Recovery of a marine community from the Messinian Salinity Crisis

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With 2 figures and 4 tables

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Abstract: Paleocological analysis of the reef community shows that, apart from corals, it was dominated by epifaunal molluscs. It represents one of the most diverse fossil communities found on Cyprus following the Messinian Salinity Crisis (MSC), with 38 identified species of macrofossils and 8 species of foraminifera. When compared to patch reefs on Cyprus formed just prior to the MSC, this Pliocene reef shows both the biological devastation of the event and the quick and complete recovery of the reefal biodiversity.

Zusammenfassung: Eine Korallenriffgemeinschaft wurde in der Nicosia-Formation (Pliozän) in Zentral-Zypern gefunden. Sie stellt das erste solche Riff aus dem Postmessinian der Insel dar. Die Erstbesiedlung des weichen Schlammes wurde durch eine Lage aus flachen Austern und Pectinidenschalen ermöglicht. Mit 38 Makrofossil-Arten und 8 Foraminiferen-Arten stellt die Fauna eine der diversesten Gemeinschaften aus dem Postmessinian der Insel dar. Die Riffgemeinschaft wurde, außer von Korallen, durch Muscheln dominiert. Sie lebte in etwa 40 Meter Tiefe bei 20° bis 25° C. Im Vergleich zu Patchreefs vor der Messinian Salinity Crisis zeigt dieses Pliozänriff die rasche und zerstörerische Wirkung des Events (wahrscheinlich überlebten überhaupt keine Riff-Arten auf Zypern) und die schnelle und vollständige Erholung der Riff-Diversität nach dem Ereignis.

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Introduction

The island of Cyprus, located in the eastern Mediterranean, is characterized by the Cretaceous Troodos ophiolite, which was emplaced by uplift in the Tertiary and Quaternary. In addition to exposing the pseudostratigraphy of the Troodos ophiolite, this uplift also revealed the sediments deposited on top of the ophiolite complex. Many of these sedimentary units are well exposed in the Mesaoria Basin north of the Troodos ophiolite, allowing for convenient examination of their sediments and fossils.

Following the Messinian salinity crisis of the Late Miocene, the Mediterranean Basin refilled with sea water and the marine conglomerates, sandstones, and silts of the Nicosia Formation were deposited on top of the evaporitic gypsums in the Mesaoria Basin of Cyprus. These marine deposits mark the return of open marine conditions to the Mesaoria Basin, between the Troodos Massif and the Kyrenia Range (Fig. 1). The sediments of the Nicosia Formation are derived from the erosion of the Troodos Massif, the only part of Cyprus then above sea level (McCallum & Robertson 1990). Many fossils, mostly bivalves, gastropods, and foraminiferans, are well preserved in the silts of the Nicosia Formation. These fossils record the repopulation of the Mesaoria Basin following the Messinian Salinity Crisis, providing a unique opportunity to study the recovery faunas.

Eight distinct paleocommunities have been identified by the authors in the Nicosia Formation south and southwest of the village of Meniko on the central Mesaoria Plain, each with unique guild structures and species. Most are dominated by epifaunal filter feeders and all contain the common oyster *Ostrea*. One of these paleocommunities consists of a remarkably well-preserved coral reef ecosystem. The branching coral *Cladocora* serves as the framework for this reef, which is built on the shells of *Ostrea* and the pectinid bivalve *Chlamys*. Once this reef community was established, a diverse array of bivalves and gastropods inhabited it, with some appearing to be ecologically dependent on *Cladocora*. This succession from an *Ostrea* and *Chlamys* dominated community to a diverse coral reef community represents the recovery of a community after the Messinian Salinity Crisis.

These Pliocene paleocommunities, the coral reef included, also demonstrate how few Miocene taxa in the Mediterranean survived the crisis. So few survived, in fact, that it seems likely that there were no refuges for marine invertebrates in the Mediterranean Basin during the Messinian salinity crisis. It still remains to be seen, however, whether or not the Mediterranean Basin was repopulated from only the Atlantic Ocean or whether some taxa from the Indo-Pacific also participated.

It should be noted that the pre- and post-crisis faunas of Cyprus can easily be compared to one another because they are preserved in formations with

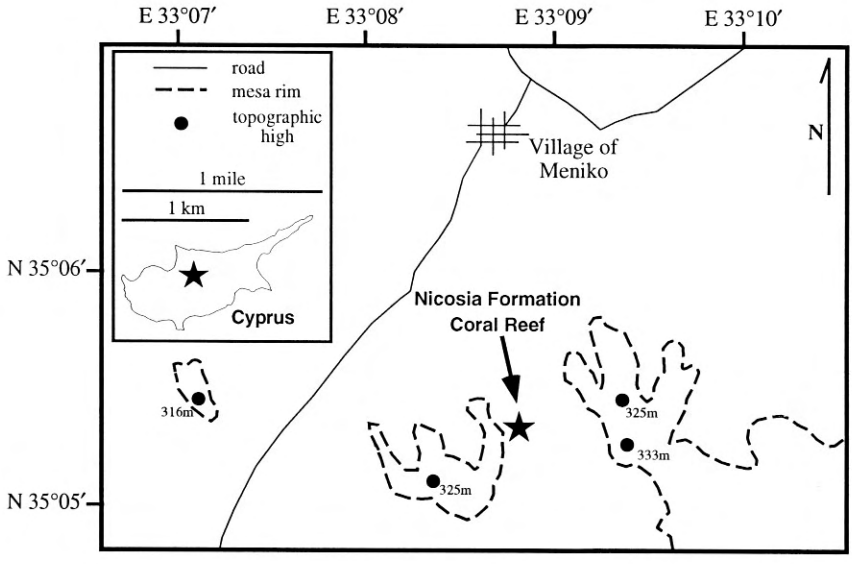

Fig. 1. Location of the Nicosia Formation (Pliocene) coral reef on the Mesaoria Plain of central Cyprus.

similar depositional environments. Both the Miocene Pakhna Formation and the Pliocene Nicosia Formation are primarily composed of silts deposited in low energy shallow marine environments, and their exposures are nearly indistinguishable. The Pakhna Formation is overlain in places by the evaporitic gypsums of the Kalavasos Formation, while the Kalavasos Formation is overlain by the Nicosia Formation (Fig. 2). This stratigraphic relationship makes the Pakhna and Nicosia Formations excellent recorders of the pre- and post-crisis faunas on Cyprus.

Geologic setting and stratigraphy

In the Late Cretaceous, approximately 85 to 92 million years ago, the rocks of the Troodos Massif of Cyprus were formed as new oceanic crust during the opening of a small ocean basin north of Gondwana (Moores & Vine 1971, Robertson & Dixon 1984, Mukasa & Ludden 1987). Spreading did not last long, however, and soon a fragment of the Troodos microplate was

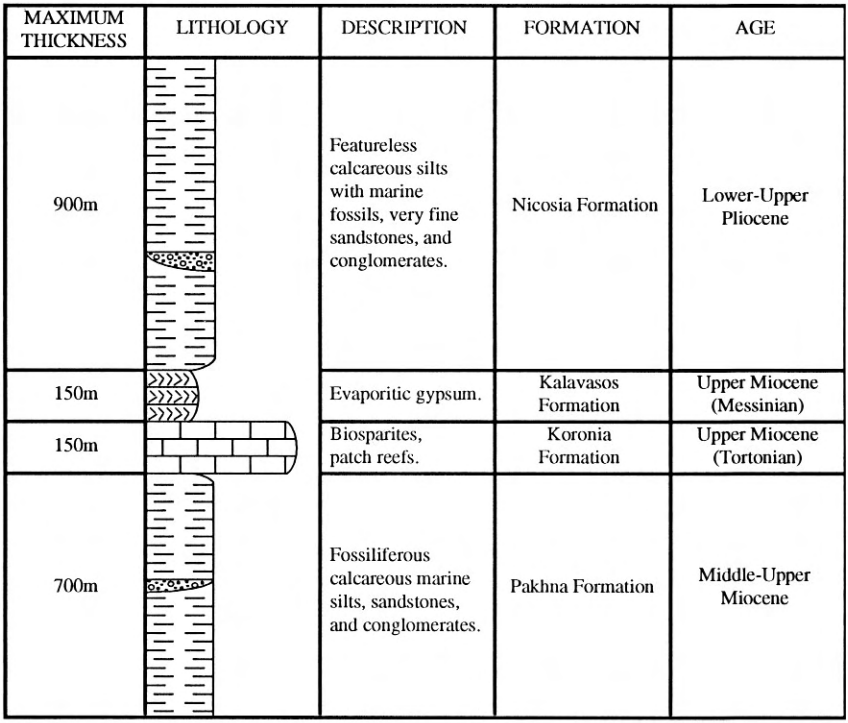

Fig. 2. Stratigraphic column of the Nicosia Formation and associated units exposed on the Mesaoria Plain of central Cyprus.

rotated approximately 90° by a complex strike-slip lineament (Clube et al. 1985). Pieces of the continental margins bordering the Troodos microplate were rotated in conjunction with what is today the Troodos Massif. These pieces of continental crust formed the Kyrenia and Mamonia terranes of Cyprus (McCallum & Robertson 1990).

The Troodos microplate and its accompanying terranes remained at the bottom of a chalk-depositing sea until the Miocene, when the Troodos Massif first emerged above sea level, possibly as a result of uplift from the

subduction of Africa under Eurasia at a subduction zone south of Cyprus (McCallum & Robertson 1990). The Mesaoria Basin began to form in the Early Miocene as a half-graben bordered by normal faults on its north and south margins, with relative uplift of its southern margin and subsidence along its northern margin, south of the still-submerged Kyrenia Terrane. During this time, the reef deposits and marls of the Koronia and Pakhna Formations were deposited, followed in the Late Miocene by the evaporite gypsums of the Kalavasos Formation, deposited during the Messinian salinity crisis. Directly on top of the Kalavasos Formation gypsums lie the silts of the Nicosia Formation, the first marine sediments deposited in the Mesaoria Basin following the Messinian salinity crisis (McCallum & Robertson 1990) (Fig. 2).

Within the silts of the lower Nicosia Formation are a number of Troodos-derived conglomerate lobes composed of subangular to subrounded clasts of igneous composition and numerous shell fragments. These conglomerates are in distinct channel-shaped bodies approximately 15 meters thick and hundreds of meters wide and are most likely the toes of small fan-deltas that progressed northward across the basin with the uplift of the Troodos Massif. They are the first indication of a significant uplift of the Troodos Massif, causing its first appearance as a major clastic sediment source (McCallum and Robertson 1990). The silts and very fine sands of the Nicosia Formation are extremely fossiliferous in local areas. Most of the outcrops of this part of the formation are actually barren of macrofossils, but where fossils do exist, they are abundant.

The upper Nicosia Formation shows the fining upward of the conglomerates into sand facies, reflecting a lowering in the relief of the Troodos Massif. At the same time the once pervasive silts coarsen upward into very fine sands, indicating a shallowing of the basin. Both of these changes suggest that uplift of the Troodos Massif and subsidence of the Mesaoria basin slowed significantly in the Late Pliocene. This slowing of uplift and subsidence created a relatively flat sandy platform in the Mesaoria basin that stretched between the subaerial Troodos Massif and the still submarine Kyrenia Range (McCallum & Robertson 1990).

Overlying the Nicosia Formation on the southern side of the basin are the conglomeratic sediments of the Kakkaristra Formation (Fig. 2). The Kakkaristra Formation is 10-15 meters thick and is composed of diverse facies ranging from cross-bedded conglomerates to bioturbated silts. The sediments of the Kakkaristra Formation are interpreted as a fan-delta deposit with fluvial, beach, bay, and lagoonal facies (McCallum & Robertson 1990).

Location and field description

The Nicosia Formation coral reef was discovered at N 35° 5.767', E 33° 8.925', on the west side of the large valley directly south of the village of Meniko on the central Mesaoria Plain. The framework of the reef is composed of the thin ramose coral *Cladocora*, with numerous mollusks and serpulids scattered through its branches. The reef is 9 meters thick in its thickest region near the center of the exposure. The width of the exposed reef is approximately 50 meters, with reef thickness thinning to zero at each end. The base of the reef consists primarily of *Ostrea* valves lying flat on unconsolidated, unfossiliferous clays and silts. Corals are directly attached to these valves, growing upwards. The reef was buried by similar clays and silts.

Methods

Macrofossil specimens were collected from the entire reef. Collected specimens were cleaned and identified, and the number of individual organisms present in the samples was counted. Sediment samples were also collected for foraminiferal analysis. These samples were sieved in a nest of 40, 60, and 80 mesh sieves. Foraminifera were then picked from the 60 mesh fraction of the sediment, where almost all of them were concentrated. The most abundant foraminifera were then identified, and planktic percentages were calculated for each site to use in paleobathymetric analyses. The foraminiferal assemblages were also used for paleoenvironmental analysis. Representatives of the macrofossils have been deposited in the collections of the Natural History Museum in London. The foraminifera are stored in the Department of Geology at The College of Wooster, Ohio, USA.

Paleocommunity analysis

The Nicosia coral reef paleocommunity is extraordinarily diverse, especially in comparison to the other fossil communities in the formation. It has numerous epifaunal filter feeders, semi-infaunal filter feeders, epifaunal predators, and epifaunal herbivores within a coral reef ecosystem. Over three quarters of the species in this paleocommunity, aside from the coral *Cladocora*, is composed of epifaunal filter feeders.

The dominant non-coral species of this paleocommunity are the heterodont bivalves *Chama carinata* and *Chama gryphoides* (27.0 %), the pectinid bivalve *Chlamys* sp. 1 (13.7 %), and the isodont bivalve *Spondylus* sp. (11.3 %) (Table 1). *Chama* spp., *Chlamys* sp. 1, and *Spondylus* sp. are all

Table 1. Nicosia coral reef epifaunal guilds; percentages in parentheses represent percentage of the total specimens in the Coral Reef Site paleocommunity; bold percentages represent percentage of the paleocommunity occupying that particular guild; unidentifiable specimens account for only 1.7 % of the total specimens in the paleocommunity; guilds after BAMBACH (1983).

Nicosia Formation Reef Epifauna
Attached Low Suspension Feeders
Arca noae (3.3 %)
Barbatia barbata (6.2 %)
Barbatia sp. (0.3 %)
Cardita defterensis (0.9 %)
Chama spp. (27.0 %)
Chlamys sp. 1 (13.7 %)
Chlamys sp. 2 (7.1 %)
Pseudamussium sp. (1.5 %)
Serpulids (1.5 %)
Spondylus sp. (11.3 %)
Vermetus sp. (1.5 %)
74.3 %
Attached Erect Suspension Feeders
Cladocora sp.
Reclining Suspension Feeders
Ostrea sp. (3.3 %)
3.3 %
Herbivores
Astraea rugosa (0.9 %)
Bittium sp. (0.3 %)
Calliostoma pulcrum (0.3 %)
Calliostoma zizyphinun (0.3 %)
Diodora italica (4.5 %)
Jujubinus striatus (0.6 %)
Monodonta sauciata (0.6 %)
7.5 %
Carnivores
Bolinus brandaris (0.3 %)
Buccinulum sp. (1.2 %)
Cerithium sp. (1.5 %)
Crab
Mitra carbonaria (0.9 %)
Nassarius (*Hinia*) sp. (0.3 %)
Trivia europaea ? (0.3 %)
4.5 %

epifaunal filter feeders which required a hard substrate on which to attach themselves. In fact, pieces of *Cladocora* were often found within the outer growths of the left valves of numerous *Spondylus* sp. specimens, indicating that these *Spondylus* sp. specimens were once attached to the reef itself.

Epifaunal filter feeders comprise 77.5 % of the total non-coral specimens in this paleocommunity. These epifaunal filter feeders are: *Arca noae, Barbatia barbata, Barbatia* sp., *Cardita defterensis, Chama* spp., *Chlamys* sp. 1, *Chlamys* sp. 2, *Ostrea* sp., *Pseudamussium* sp., serpulids, coral encrusting serpulids, *Spondylus* sp., and *Vermetus* sp. (Table 1). This group of epifaunal filter feeders is unique because of the low percentage of *Ostrea* sp. (3.3 %), the predominance of the attaching bivalves *Chama* spp., *Chlamys* sp. 1, and *Spondylus* sp., and the large percentage of the paleocommunity for which they account (Table 1).

Unlike the abundant epifaunal filter feeders, infaunal filter feeders account for only 4.2 % of the total specimens in this paleocommunity and are represented by *Cardium echinatum, Dosinia* sp. 2, and *Venus* (*Antigona*) *cunctata* (Table 2). Semi-infaunal filter feeders are more diverse than the infaunal filter feeders with 5 different species, but they still account for only 3.9 % of the total non-coral specimens of this paleocommunity. These five semi-infaunal filter feeders are *Anadara diluvii, Glycymeris foujasi* ?, *Striarca lactea, Turritella communis*, and *Turritella triplicata* (Table 2). The relatively low percentages of infaunal and semi-infaunal filter feeders in this paleocommunity may indicate that a suitably soft substrate for these life modes was rare in this reef ecosystem.

The seven vagrant benthic epifaunal predators present in this paleocommunity are *Bolinus brandaris, Buccinulum* sp., *Cerithium* sp., a crab, *Mitra carbonaria, Nassarius* (*Hinia*) sp., and *Trivia europaea* ? (Table 1). These epifaunal predators comprise 4.5 % of the total specimens of this paleocommunity. In addition to the crab claw tip found in the sediment sample from this site, evidence for crab predation may be present in the unusual breakage pattern of a rather large *Astraea rugosa* shell from this paleocommunity.

Naticarius punctatus (0.6 %) is the only infaunal predator in this paleocommunity (Table 2). Although naticid gastropod specimens are rare in this paleocommunity, evidence for naticid predation abounds in the numerous beveled predatory boreholes found in *Venus* (*Antigona*) *cunctata* valves at this site.

This paleocommunity has a diverse group of herbivores, with the gastropods *Astraea rugosa, Bittium* sp., *Calliostoma zizyphinum*?, *Calliostoma pulcrum, Diodora italica, Jujubinus striatus*, and *Monodonta sauciata* accounting for 7.5 % of the total specimens (Table 1). This diversity and

Table 2. Nicosia coral reef infaunal guild table; percentages in parentheses represent percentage of the total specimens in the Coral Reef Site paleocommunity; bold percentages represent the percentage of the paleocommunity occupying that particular guild; unidentifiable specimens account for only 1.7 % of the total specimens in the paleocommunity; guilds after BAMBACH (1983).

Nicosia Formation Reef Infauna
Shallow Active Suspension Feeders
Anadara diluvii (0.6 %)
Cardium echinatum (0.9 %)
Dosinia sp. 2 (0.6 %)
Glycymeris foujasi ? (0.3 %)
Striarca lactea (0.3 %)
Turritella communis (1.8 %)
Turritella triplicata (0.9 %)
Venus (*Antigona*) *cunctata* (2.7 %)
8.1 %
Carnivores
Naticarius punctatus (0.6 %)
0.6 %

abundance of herbivores may indicate that plant and algal life was common, if not abundant, in this paleocommunity.

The preservation of the Nicosia coral reef paleocommunity is astounding. Nearly all of the *Spondylus* sp. specimens are articulated and most have coral branches embedded in their left valves where they were once attached to the reef. Several *Spondylus* sp. specimens are still so firmly attached to the reef that they could not be removed for collection. Some *Arca noae* and most *Chama* spp. specimens are articulated. Many of these articulated specimens were probably close to being in life position. The external detail of all the specimens is exceptional and almost none of the specimens are broken in any way.

Paleoenvironmental analysis

The only planktic foraminiferan recovered is *Globigerinoides elongatus*. This species is biostratigraphically undiagnostic in the Pliocene. The benthic foraminiferal assemblage has *Elphidium crispum, Ammonia beccarii,*

Ammonia perlucida, Reussella spinulosa, Rosalina globularis, Asterigerina sp., and *Cibicides lobatulus* as the most abundant species.

The combination of *Ammonia beccarii* and *Rosalina globularis* at this site indicates an approximate local water temperature of 20 to 25°C (BRADSHAW 1961, SLITER 1965), and the abundance of *Cibicides lobatulus* may indicate the presence of abundant plant and algal life in this paleocommunity (BROEKMAN 1974). Also, the combination of *Elphidium* and *Asterigerina* indicates that the Coral Reef paleocommunity was located somewhere in the nearshore zone at a depth no greater than 70 meters (BOLTOVSKOY & WRIGHT 1976).

The percentage of planktic foraminifera in the coral reef assemblage is 3.6 %. Paleobathymetric analysis using WRIGHT's (1977) equation is not possible because it does not work for planktic percentages below 5 %. However, a planktic percentage of 5 % results in an estimated depth of 40 meters or less using WRIGHT's equation.

Messinian Salinity Crisis recovery and repopulation

This Pliocene Nicosia Formation patch reef can be compared to other patch reefs on Cyprus found just below the Messinian evaporites in the Koronia Formation. These reefs, like many others in the Messinian Mediterranean, were dominated by the scleractinian coral *Porites* and coralline algae of several types (FOLLOWS & ROBERTSON 1990, FOLLOWS 1992, MANKIEWICZ 1995, REINHOLD 1995). The Nicosia reef is comparable in diversity and structure to its pre-salinity crisis counterparts in the Koronia Formation, but taxonomic studies of previous work by COWPER-REED (1935a) reveal that only 13 % of the species in the pre-crisis Koronia reefs are also present in the Nicosia reef. The crisis devastated the reef communities on Cyprus, but they were quickly replaced by similar guilds with almost entirely different species within them.

The Koronia reefs were formed on fault blocks of basalts and conglomerates which provided hard substrates for the *Porites* coral and coralline algae (FOLLOWS & ROBERTSON 1990, FOLLOWS 1992). The Nicosia reefs also depended upon a fortuitous hard substrate in an otherwise muddy environment. The large numbers of flat *Ostrea* valves provided a patch of stable and hard substrate, enabling *Cladocora* to establish a foothold and develop the reef framework. *Ostrea* appears to have opportunistically colonized the soft muds in abundance, facilitating the growth of the reef and vastly increasing the local biodiversity. A similar facilitation of reef initiation by imbricated oyster valves was noted by INSALACO (1996) in Upper Jurassic reefs of northern France.

Table 3. Koronia coral reef epifaunal guild table; species also present in the Pliocene *Cladocora* reef of the Nicosia Formation are marked with an asterisk (*); species data from COWPER REED (1935a); guilds after BAMBACH (1983).

Koronia Formation Reef Epifauna
Attached Low Suspension Feeders
Arca noae *
Barbatia barbata *
Cardita aculeata
Cardita koroniensis
Chama gryphina
Chama gryphoides *
Chama sp.
Chlamys convexior
Chlamys sp. *
Chlamys submalvinae
Chlamys tauroperstriatus
Exogyra sp.
Lima lima
Pecten northamptoni
Pecten sp.
Septifer oblitus
Serpulids
Spondylus concentrus
Attached Erect Suspension Feeders
Porites sp.
Reclining Suspension Feeders
Ostrea sp.
Herbivores
Cidaris melitensis
Diodora italica *
Fissurella sp.
Haliotis tuberculata
Trochus patulus
Trochus rotellaris
Trochus sp.
Carnivores
Cerithium cyprinum
Cerithium kavasiense
Cerithium koroniense
Cerithium laevisubuloides
Nassa sp.
Tenagodes anguinus

Table 4. Koronia coral reef infaunal guild table; species also present in the Pliocene *Cladocora* reef of the Nicosia Formation are marked with an asterisk (*); species data from Cowper Reed (1935a); table format after Bambach (1983).

Koronia Formation Reef Infauna
Shallow Passive Suspension Feeders
Lithophaga lithophaga
Shallow Active Suspension Feeders
Anadara diluvii *
Astarte sp.
Cardilia michelotti
Cardium andreae
Cardium arcella
Cardium edule
Cardium multicostatum
Cardium sp.
Circe minima
Limopsis anomala
Lucina reticulata
Lucina sp.
Mactra sp.
Meretrix sp.
Miltha sp.
Striarca lactea *
Tapes basteroti
Tapes decussatus
Tapes geographica
Turritella subangulata
Turritella turris
Venus basteroti
Venus ovata
Venus sp.
Shallow Active Deposit Feeders
Dentalium sp.

A comparison of the guild structure of the Nicosia reef and the Koronia reefs reveals striking similarities. The epifauna of both reef communities are dominated by attached suspension-feeding bivalves (Tables 1 and 3). Several genera of these bivalves, namely *Cardita, Chama, Chlamys*, and *Spondylus,*

are common to both communities. The species *Arca noae, Barbatia barbata, Chama gryphoides*, and *Chlamys* sp. are found in both communities as well, indicating their survival of the Messinian Salinity Crisis.

Both communities also contain abundant herbivorous and carnivorous gastropods (Tables 1-4). Only one of these species, the fissurellid gastropod *Diodora italica*, is common to both communities. The genus *Cerithium* is common to both communities as well.

Aside from presence of the deposit-feeding echinoid *Psammechinus* in the Koronia reefs, the epifaunal guilds occupied by the Nicosia and Koronia reefs are identical (Tables 1 and 3). Even while there are no percentages in the Koronia epifaunal guild table, the relative number of species in each guild is similar between the Nicosia reef and the Koronia reef.

Structural similarity is also displayed in the infaunal guild tables of both communities. Both communities are overwhelmingly dominated by shallow active suspension feeders (Tables 2 and 4). In both cases, these suspension feeders are mostly burrowing bivalves with some turritellid gastropods also present. Shared genera abound in this guild, with the genera *Cardium, Glycymeris, Turritella*, and *Venus* common to both communities. On the species level, the arcid bivalves *Anadara diluvii* and *Striarca lactea* are found in both communities. The deposit-feeding scaphopod *Dentalium* and the rock-boring bivalve *Lithophaga lithophaga* represent two guilds unique to the Koronia reefs.

The similarity of their epifaunal and infaunal guild structures indicates that the Nicosia reef, while not as diverse as the Koronia reefs, represents a nearly full ecological recovery following the Messinian Salinity Crisis. This relatively rapid ecological recovery was performed by almost entirely different species than were present before the crisis, displaying both the devastation of the Messinian Salinity Crisis and the rapidity, at least in one case, of its recovery.

Conclusions

1. A patch reef of *Cladocora* sp. was formed on an oyster shell layer which stabilized an otherwise soft muddy substrate in central Cyprus during the Pliocene.

2. The dominant non-coral species preserved in the reef are the heterodont bivalves *Chama carinata* and *Chama gryphoides*, the pectinid bivalve *Chlamys* sp. 1, and the isodont bivalve *Spondylus* sp., all of which were epifaunal filter-feeders which required hard substrates.

3. The coral reef paleocommunity had an estimated local water temperature of 20 to 25°C, at an approximate depth of approximately 40 meters or less.

4. The reef was eventually buried by the same type of silts and muds on which it was originally recruited.
5. When compared to patch reefs on Cyprus formed just prior to the Messinian Salinity Crisis, this Pliocene reef shows both the biological devastation of the event (only 13 % of Miocene reef species appear afterwards on Cyprus) and the quick recovery of reefal biodiversity.

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