INVERTEBRATE PALEONTOLOGY OF ISRAEL
AND ADJACENT COUNTRIES

WITH EMPHASIS ON THE TRIASSIC
AND JURASSIC BRACHIOPODA

INVERTEBRATE PALEONTOLOGY OF ISRAEL
AND ADJACENT COUNTRIES

WITH EMPHASIS ON THE TRIASSIC AND JURASSIC BRACHIOPODA

Howard R. FELDMAN, Ph.D.

Biology Department
Lander College for Women
The Anna Ruth and Mark Hasten School
A Division of Touro College

Research Associate,
Division of Paleontology (Invertebrates),
American Museum of Natural History,
New York, NY

New York 2013

Library of Congress Cataloging-in-Publication Data:
A catalog record for this book is available from the Library of Congress.

ISBN 978-1-61811-305-4 (hardback)
ISBN 978-1-61811-306-1 (electronic)

Published by Touro College Press and Academic Studies Press.
Typeset, printed and distributed by Academic Studies Press.
Cover design by Ivan Grave

Touro College Press
Michael A. Shmidman and Simcha Fishbane, Editors

43 West 23rd Street
New York, NY 10010, USA
touropress.admin@touro.edu

Academic Studies Press
28 Montfern Avenue
Brighton, MA 02135, USA
press@academicstudiespress.com
www.academicstudiespress.com

For my wife Susan for her understanding, great patience, support and tolerance, despite my having taken over the house with thousands of fossil specimens, each one of which is unique and tells a story.

TABLE OF CONTENTS

FOREWORD

It has been a real pleasure to review Dr. Howard R. Feldman's published record! His contributions to basic geological-paleontological science are very meritorious. I first came in contact with Dr. Feldman when he was working on his graduate degree in paleontology, centered on the study of Devonian brachiopods from New York. At that time I was favorably impressed by his diligence, and his rapidly developing capabilities in basin paleontology and stratigraphy. The promise of these early years has been fulfilled now in his professionally mature years. After his initial baptism working with Devonian brachiopods, he took advantage of the opportunity to do field work, fossil collecting and stratigraphy in the Jurassic of the Middle East, the Sinai Peninsula and southern Israel in particular. Fruitful collaboration with the appropriate Israeli geologists and careful work on resulting brachiopod collections from Sinai and Israel, along with some material from Jordan, has resulted in a series of publications. These publications feature detailed, critical morphology (including ontogenetic information when available), and taxonomy of the brachiopods, plus mature consideration of their paleontology and biogeography. Feldman's work pays careful attention not only to material collected by him, but also critical attention to the earlier work of others in this area, updating the older work and leaving no stone unturned in the effort to place both his own material and those previously published by others in their proper context. Additionally, his paleoecological work on the community paleoecology of his materials is exemplary, as is his work on associated trace fossils in the faunas.

Feldman is now a very well rounded professional, adept not only in carefully describing Mesozoic brachiopods, but also evaluating their biogeographic, paleoecologic and paleogeographic implications. Feldman is one of the very small numbers of paleontologists today capable of effectively studying and publishing on Mesozoic brachiopods; I can think of no one else in North America thus occupied; he has earned an important position in our profession.

Arthur J. Boucot, Ph.D.
Department of Zoology
Oregon State University

INTRODUCTION

Much of the groundwork for paleontologic research in the Levant and Sinai was conducted by scientists of the Geological Survey of Israel. What follows is a brief summary of some important studies by those scientists and others that dealt mainly with faunas in Israel and Sinai and laid the foundation for future research, particularly on the invertebrate faunas.

The Geological Survey of Israel (GSI) was established in 1949 (Grader and Reiss, 1958). This event represented a major step toward building up the country's economy in that it helped develop its natural resources, such as oil, gas and minerals. Grader and Reiss reported that in 1958 the GSI was made up of seven divisions: Geochemistry, Hydrogeology, Mapping, Mineralogy, Oil, Paleontology and Seismology & Geomorphology. Today The GSI is organized into six divisions: Directors Office, including Administration and Logistics, Water and Mineral Resources, Geochemistry and Environmental Geology, Geological Mapping and the Subsurface Environment, Engineering Geology and Geological Hazards, and Earth Sciences Information Systems.

The Paleontology Division of the Geological Survey of Israel, headed by Professor Zeev Reiss in 1959, was divided into micropaleontology and megapaleontology sections. Its research program was important in contributing to various aspects of early geological exploration in Israel, including the mapping program, water, oil and mineral exploration (Grader and Reiss, 1958). For example, Reiss and Issar (1961) reported on subsurface Quaternary correlations in the Tel Aviv area and described six stratigraphic complexes each of which was characterized by a distinct assemblage of foraminiferans. In the 1950s there were relatively few publications by scientists of the Geological Survey of Israel on the megafaunas of the country (see for example Avnimelech, 1952; Avnimelech et al., 1954; Remy and Avnimelech, 1955; Parnes, 1958).

In the 1960s, Parnes (1961, 1963, 1964, 1965) described *Pseudopygurus* Lambert from southern Israel, Coniacian ammonites from the Negev and a Middle Jurassic fauna from Makhtesh Ramon, also in the Negev. Lerman (1960) described Triassic pelecypods from southern Israel and Sinai. Avnimelech (1961) reported on a pachydiscid ammonite from Campanian chert of Israel and an isocrinid fragment from the Cretaceous of the upper Galilee. Freund (1961) reported on the distribution of Lower Turonian ammonites from Israel and neighboring countries and Freund and Raab (1969) described Lower Turonian ammonites from Israel. Raab (1962) described Jurassic-Early Cretaceous ammonites from the southern coastal plain. Lewy wrote a series of papers on ammonites from southern Israel (1967, 1969a, 1969b). Mishnaevsky (1966, 1967) studied the ostreides in the Cenomanian of central and southern Israel and Egypt. Reiner (1968) wrote on the Callovian gastropods from Hamakhtesh Hagadol in southern Israel in which he described twenty nine species including one renamed and three new species.

In the 1970s the exploration of Gebel El-Maghara, northern Sinai, enabled the scientists of the Geological Survey of Israel to study this vast and geologically diverse area. Eighteen papers were presented at the 1972-73 seminar of the Geological Survey of Israel edited by Gill (1974). The topics covered included: metamorphic rocks (Shimron, 1974), stratigraphy and structure (Bartov, 1974; Hildebrand, 1974; Shirav, 1974), sedimentology (Levy, 1974), mineralogy and geochemistry (Gavish, 1974). However, in the early part of the 1970s there is a noticeable absence of research on the megafauna of Sinai due to the political situation. Research on megafossils in Israel was accomplished by Lewy (1972, 1973, 1976, 1977), Lewy and Samtleben (1979), Parnes (1971), Bein (1976) and increased in the middle to latter part of the 1970s (Hirsch, 1976, 1977a, 1978, 1979; Parnes, 1974, 1975, 1977), especially with regard to the molluscs, specifically the bivalves, gastropods and cephalopods. However, the brachiopod faunas remained unstudied. Work was begun on the Sinai faunas in the 1980s, facilitated by the construction of a stratigraphic section of the Jurassic rocks in Gebel El-Maghara (Goldberg et al., 1971), that allowed for the subsequent study of the brachiopods and molluscs of that important section (Feldman, 1987, Feldman and Owen, 1988; Feldman, et al., 1991; Hirsch, 1978). In addition to the research in the Sinai Peninsula, Friedman et al. (1979) described pinnacle reefs of Cretaceous age exposed along the western margin of the Dead Sea.

Hirsch (1980) described the Jurassic bivalves and gastropods from southern Israel (Hamakhtesh Hagadol) and northern Sinai (Gebel El-Maghara) in which he noted their position within the Ethiopian Province (along the southern Tethyan margin). Parnes (1980) described gastropods and a brachiopod species (*Gibbirhynchia*) from the Liassic of Makhtesh Ramon and a megafauna from the Mahmal Formation (Bajocian) of the same area. Parnes (1986) described Middle Triassic cephalopods from the Negev (Israel) and Sinai (Egypt) and Lewy (1981, 1982 and 1985) wrote a series of papers on the cephalopods and molluscs of the Middle East. Lewy and Honig (1985) also described a Late Coniacian ammonite from the lower part of the Sayyarim Formation near Elat (southern Israel). Marquez-Aliaga and Hirsch (1988) studied the migration of Middle Triassic bivalves in the Sephardic Province. Parnes et al. (1985) reported on new aspects of Triassic ammonoid biostratigraphy, paleoenvironment and paleobiogeography in southern Israel, also within the Sephardic Province.

Feldman and Brett (1997a, 1997b, 1998) reported on the paleoecology of Jurassic crinoids from Hamakhtesh Hagadol, southern Israel and described epi- and endobiontic organisms on crinoid columnals. They extended the range of the trace fossil *Tremichnus* (now known as *Oichnus*) by 100 million years. Hirsch et al. (1998) published a study on the Jurassic of the southern Levant that discussed the biostratigraphy, paleogeography and cyclic events of the region. Feldman (2002, 2005) described Triassic brachiopods from Makhtesh Ramon, southern Israel, and Lewy (1995) reported on Cretaceous rudists and ostreids (1996). Hoff (1998) described Late Cretaceous stomatopods from Israel and Jordan.

Triassic

The Triassic is exposed in Har Arif and Gebel Areif en-Naqa as well as the Ramon crater, Makhtesh Ramon, in the central Negev where a more complete section crops out ranging from Olenekian through Carnian stages. Borehole data and measurements from surface outcrops indicate that the thickness of the Triassic rocks in Israel ranges from 500-1100 m (Druckman, 1974; Feldman, 2002, 2005). The columnar section includes the Negev Group (Yamin and Zafir formations; Weisbrod, 1969, 1976) and Ramon Group (Ra'af, Gevanim, Saharonim and Mohilla formations; Zak, 1963). The section in Makhtesh Ramon consists of carbonates, sulfates, sandstones, siltstones, clays, that is largely clastic in the lower, more carbonate-rich in the middle and more evaporitic in the upper part (Druckman, 1969, 1974, 1976; Feldman, 2002, 2005) and ranges in age from Scythian (Early Triassic) to Carnian-Norian (Late Triassic). My work centers on the Middle Triassic transgressive Saharonim Formation that flooded most areas on the African-Arabian platform. Along the southern Tethyan margin there is a record of endemic taxa that characterized the Sephardic Province (Benjamini et al., 2005). The Sephardic Province (Hirsch, 1972) is represented along this margin and seems to be correlative with the western Mediterranean Muschelkalk and other strata in North Africa and the Levant (Benjamini et al., 2005; Hirsch, 1977b).

Early research on the Triassic was accomplished by the British Petroleum Company during World War II (Shaw, 1947), but data became available to workers only after oil companies and governments published the results of their drilling and exploration (Picard and Flexer, 1974). Future work in the Triassic involves the search for brachiopods in the sedimentary deposits in Makhtesh Ramon and the study of this generally neglected time period, at least in terms of brachiopod evolution and paleoecology.

Jurassic

In 1978 I first began to investigate the brachiopod faunas of Israel and the Sinai after attending the International Symposium on Sedimentology in Jerusalem. Dr. Francis Hirsch first introduced me to the Jurassic sequence at Gebel El-Maghara, northern Sinai, by organizing an expedition from the Geological Survey of Israel that included oil geologists, stratigraphers and paleontologists. The paper on *Septirhynchia* from the 2,000 m section at Gebel El-Maghara represents the first modern study of the brachiopod faunas of the region since the early twentieth century works of Douvillé (1916, 1925) and Cossmann (1925).

The goal of this research is to taxonomically study and revise the brachiopod faunas and investigate the ecological relationships in the various marine communities, particularly their structure and paleoecology. As data accumulates, the history of brachiopod species and their evolution within the Ethiopian Province and Tethyan margin will be elucidated. These data will provide a basis for the interpretation of the biogeographic history of the Ethiopian Province as well as insight into the structure and paleoecology of its marine communities (see, for example, Feldman and Brett 1998; Wilson, et al. 2008, 2010).

Endemic brachiopods taxa such as *Somalirhynchia africana, daghanirhynchia daghaniensis, Somalithyris bihendulensis, Striithyris somaliensis, Bihenithyris barringtoni,* and *B. weiri* were recognized by workers (Weir, 1925; Muir-Wood 1935) in the early to mid-twentieth century. Cooper's (1989) work on the Jurassic brachiopods of Saudi Arabia was based largely on collections made during the years 1933-1953 by field geologists of the Arabian-American Oil Company (Aramco) and the Kier-Kauffmann collections (1962) (see Feldman et al., 2001, for a more detailed discussion). His data, combined with the data collected from Sinai, Israel, and Jordan over the last several years, aid in establishing areas of endemism within the Ethiopian Province. Endemic faunas in the ammonoid Cephalopoda were recognized by Arkell (1952, 1956) and Kitchin (1912) found endemics within the trigoniacean and crassatellacean bivalves. These endemics also helped define the Ethiopian Province. Today, after decades of compiling mostly brachiopod data and revising the taxonomy of the brachiopods found within this province, we have a clearer picture of the extent of the endemism that typifies these faunas. The faunas of Israel and Jordan lie at the northernmost part of the Indo-African Faunal Realm and may therefore be related to faunas of the Tethyan Realm. Completion of a systematic revision of Israeli, Jordanian and Egyptian (Sinai) Jurassic brachiopods will enable us to define faunal- and province-realm boundaries with greater accuracy.

Very few of Cooper's (1989) species found in Saudi Arabia, collected from seven formations (Marrat, Dhruma, Tuwaiq Mountain, Hanifa, Jubaila, Arab and

Hith) and representing 1126 meters of sediment, occur in the Negev region; they are more closely related to the Sinai faunas. The Negev fauna appears to be more akin to Muir-Wood's (1935) and Weir's (1925) Somalia material. Additionally, Cooper has erected many new species and I strongly suspect that many of these are simply varieties. Shi and Grant (1993) revised some Jurassic rhynchonellids but did not deal with the distribution of genera and species, except in a general sense. They reported on taxa mostly from the United Kingdom, France, China, India, Egypt but only one from Israel. Only four genera (*Globirhynchia, Burmirhynchia, Somalirhynchia,* and *Pycnoria*) occurred within the Jurassic Ethiopian Province.

The data collected from studies on the Jurassic of Israel, Jordan and Sinai, along with data from future projects, will help determine how closely the brachiopod faunas of the Middle East can be correlated with those of other regions within the Tethyan Realm. Kitchin (1900) described a brachiopod fauna from the Jurassic limestones of the Cutch, India, in which he broadly correlated the Putchum and Charee groups with the Bathonian to Kimmeridgian of Europe. Arkell (1956) suggested that the Putchum Beds represented the Lower Callovian whereas the Charee ranged from the Upper Callovian to Oxfordian. Until now only a broad comparison with the Cutch faunas and the Ethiopian Province faunas was possible. However, with additional collecting in Israel it will be possible to correlate the stratigraphic sections and determine the taxonomic and paleogeographic relationship of the faunas. I suspect that many genera and species from Saudi Arabia, the Cutch and Israel are very closely related, but lack of sufficient material has made exact determinations impossible. For example, the rhynchonellids described by Kitchin (1900) as *Rhynchonella fornix* and *R. nobilis* are probably congeneric with the rhynchonellid *Pycnoria* described by Cooper (1989) from the Upper Bathonian to Lower Callovian of Saudi Arabia. Kitchin's *R. versabilis*, also from beds equivalent to the Upper Bajocian, are similar to those named and described by Cooper (1989), from an equivalent horizon, as *Globirhynchia crassa*. The genus *Schizoria* described by Cooper (1989) from the Dhruma Formation of Saudi Arabia shows affinities to *R. assymetrica* from the Charee Group at Jooria, India. Many terebratulids also seem to have congeneric forms on both continents. *Kutchithyris* species, similar in external morphology to those from the Cutch, have been described from both Israel and Saudi Arabia.

Some monographs (Weir, 1925, 1929; Muir-Wood, 1935), while dealing with specimens in strata ranging from Bajocian to Kimmeridgian age, give the impression of a rhynchonellid-dominated fauna of comparatively little diversity occurring in beds of Middle to Upper Jurassic age in Somalia. Beds of similar age (Dubar, 1967) from Tunisia also deal more thoroughly with the rhynchonellid rather than the terebratulid species. The conclusion drawn from such publications has produced an impression of a closer faunal and possibly ecological relationship of these areas. Likewise, areas currently being studied in beds of Bathonian to Oxfordian age in the Negev, Israel, suggest a closer comparison with the Somali fauna than with Cooper's (1989) Saudi Arabian fauna. Yet, there are a number of terebratulid species that occur in both Saudi Arabia and Israel that have not been noted from Somalia or Tunisia. Preliminary comparisons with the Israel faunas have shown that some genera from Saudi Arabia have not yet been discovered in the Negev, Somalia or Tunisia.

Paleobiogeographic data obtained from analysis of the brachiopod faunas in the Levant and Egypt will also provide insight into the sequence of rifting within the southern Tethyan Platform that led up to total isolation of the Ethiopian Province from its northern boreal counterpart by the completion of the Tethyan-North Atlantic Ocean divide. Work on the geographic distribution of brachiopod genera and species in the areas discussed above is in progress and more comparative work, especially between the faunas of Saudi Arabia and Israel, as well as those of Madagascar and the Cutch, must be done before any real attempt at closer correlation can be achieved.

Community Ecology

The Jurassic was a critical time in the evolution of marine benthic communities. The "Mesozoic Marine Revolution" (Vermeij, 1977, 1987) began then in earnest as ecological systems recovered from the devastation of the Permo-Triassic extinctions and communities took on more modern aspects with a rise in predators and a consequent infaunalization of many taxa on both soft and hard substrates. This Jurassic diversification has been described both very broadly (e.g. Sepkoski, 1977) and in numerous systematic studies of particular clades, but it is still little known at the community level. The analysis of well-preserved and well-exposed Jurassic marine invertebrate assemblages in the Negev, southern Israel, will help fill the gap in paleoecological studies and answer a set of paleogeographic and biostratigraphic questions as well. Future studies will integrate a community analysis of brachiopod-dominated and hard substrate communities within a sequence stratigraphic framework and correlate various Jurassic beds throughout the Ethiopian Province from North Africa to Saudi Arabia.

Furthermore, hard substrate communities inhabited by sclerozoan (those organisms which live on or in hard substrates such as hardgrounds, shells and other skeletons) develop under very distinct physical requirements of temperature, water depth, nutrient levels and so forth. Wilson et al. (2008) noted that marine fossil sclerozoans are commonly found on hardgrounds (synsedimentarily-cemented seafloor sediments), rockgrounds (exposed surfaces of rocks lithified much earlier), and various biotic substrates including carbonate skeletons, wood and other plant materials. Since they are almost always preserved in situ, they are excellent paleoenvironmental indicators. The proximity of individual elements in hard substrate communities are also preserved intact, including overlapping competitive relationships, commensalism, and predatory borings. These communities are easily compared with each other over time and space, so they have been very useful for evolutionary paleoecological studies (Taylor and Wilson, 2003). Sclerozoan abundance and diversity increased worldwide during the Jurassic (Taylor and Wilson, 2003; Wilson et al., 2008), probably due to the increase in carbonate hard substrates in shallow marine environments including hardgrounds (Palmer, 1982; Wilson et al., 2008) and thick carbonate skeletons such as those of oysters, sponges and corals (Stanley and Hardie, 1998; Wilson et al., 2008). The hard substrate faunas of the tropical Ethiopian Province have not yet been thoroughly described and integrated with other better known subtropical to temperate faunas in Europe and North America.

One very significant study in the Negev was that of a detailed description of bioerosion, that is, the removal of consolidated mineral or lithic substrate by the direct action of organisms as defined by Neumann (1966) and revised by Wilson et al. (2010) to signify the destruction of hard substrates by biological processes. Here numerous patch reefs and crinoids were bioeroded by various invertebrates. The significance of the discovery of these ichnospecies is that it is the first equatorial Middle Jurassic boring ichnofauna to be documented (Wilson et al. 2010).

In order to provide useful data for evolutionary, paleoecological and stratigraphic studies, the computation of "best-fit" correlation lines for several local sections within the Negev will be completed along with the construction of a composite standard (Shaw, 1964) that can also be used for intercontinental correlation (based on genera). A composite standard nearly always produces a much clearer picture of relative times of origin and extinction of species than can be provided by any single section and its use, therefore, makes recognition of evolutionary lineages and phylogenetic relationships less speculative than they would otherwise be (Raup and Stanley, 1978). In addition to biostratigraphic information, I have found other diverse data (e.g., an oolitic limestone [marker] bed that extends laterally throughout the study area in Hamakhtesh Hagadol) that would strengthen the conclusion of a strictly biostratigraphic investigation.

In future work sequence stratigraphic analysis will be used as a check on biostratigraphic correlation and as a means of integrating facies information. Fossils are the primary tools of chronostratigraphy, and biostratigraphy enables inter-regional correlation of depositional sequences; sequence stratigraphy also permits, in turn, much more detailed resolution of time within biozones (Brett, 1995). Brett (1995) believes that the sequence stratigraphic paradigm makes a number of predictions about stratigraphic pattern and its relationship to sea level, subsidence, and sedimentation processes. He notes that on the basis of sequence stratigraphy, further deductions can be made about the distribution of both lithologic and paleontologic aspects of strata. Sequences record fluctuations of a number of parameters, such as relative sea level and sedimentation rates, which are of critical importance in governing the local distribution of ancient organisms. Many of these aspects remain incompletely explored, but the sequence stratigraphic model provides a powerful heuristic tool for investigating pattern in life history (Brett, 1995). Paleoecological analysis of the fossils collected will enable me to study the many genetic relationships between fossil distributional patterns and depositional sequences because paleoecological changes are closely correlated with fluctuations in sea level and sedimentation. Brett (1998) argues that sequence stratigraphy provides a temporally constrained framework for the evaluation of ecological and evolutionary events and, for example, may permit precise evaluation of the timing of immigration, extinction or origination of new taxa in a region or on global scales.

Topics

The first section of the book deals with some Triassic brachiopods of Makhtesh Ramon, a large erosional crater in the Negev adjacent to the town of Mitzpe Ramon. A new species of the terebratulid brachiopod, *Coenothyris oweni*, is erected and described (Feldman, 2002). The specific epithet, *oweni*, was given in honor of Ellis F. Owen, for his important contributions to the study of Mesozoic brachiopods. A second paper (Feldman, 2005) describes the ecology, taphonomy (burial) and biogeography of a marine community consisting predominantly of *Coenothyris* shells and ten genera of bivalves that were apparently smothered by pulses of clay sedimentation.

The second section of this study includes papers that deal with the Jurassic brachiopods and brachiopod-dominated communities of northern Sinai, specifically Gebel El-Maghara, Gebel Engabashi and Gebel El-Minshera (Feldman et. al., 1982). The second paper in this series (Feldman, 1987) is a study of the rare Callovian brachiopod *Septirhynchia hirschi* collected from Gebel El-Maghara in 1978. Due to silicification of the shell, the specimens were extremely well-preserved and impervious to the muriatic acid in which they were prepared, resulting in the dissolution of the limestone matrix. The acid bath technique allowed me to study the interiors without resorting to the use of transverse serial sectioning. This was followed by a description of *Goliathyris lewyi*, a new genus and species of terebratulid from Gebel El-Minshera (Feldman and Owen, 1988). In the early 1990s (Feldman et al., 1991), a study of a section of the sequence (2,000 m) at Gebel El-Maghara was published. This work included 15 brachiopod species, including four new species, from an area that is critical to understanding endemic faunas of the region (e.g. Saudi Arabia, Israel and Jordan). A follow-up study on the fauna of Gebel Engabashi within the Maghara anticline (Feldman et al., 2012) provided more data on six species (one new genus and two new species) that further elucidated the paleobiogeography of the Ethiopian Province brachiopod faunas at the northern part of the Indo-African Faunal Realm.

The third section deals with research in Hamakhtesh Hagadol, another erosional crater, a short drive south of Be'er Sheva, the "capital" of the Negev. From the strata in Hamakhtesh Hagadol I collected 13 species of brachiopods that includes one new genus and 5 new species (Feldman et al., 2001). The rocks here consist of 206 m of sediments that are divided into 69 subunits (Goldberg, 1963) belonging to the Zohar and Matmor formations. In addition to the brachiopods, we found a shallow marine sclerozoan fauna (sclerozoans are organisms that live on hard substrates) in the Matmor Formation. In this community we found an encrusting fauna that lived in a shallow lagoon on the landward side of a coral reef which was surrounded by muddy sediments that contained echinoids, oysters and both rhynchonellid and terebratulid brachiopods (Wilson et al., 2008). Additional work in Hamakhtesh Hagadol resulted in the recognition of a Middle Jurassic coral-sponge reef community also in the Matmor Formation (Wilson, et al., 2010) that represents one of the first detailed studies of bioerosion in an equatorial Jurassic ecosystem. Feldman and Brett (1998) reported on epi- and endobiontic (now termed epizoozoans and endozoozoans) organisms on Late Jurassic crinoid columns from Hamakhtesh Hagadol. They were able to extend the range of *Tremichnus* (*Oichnus*) by almost 100 million years. This section ends with a summary of the biostratigraphy, paleogeography and cyclic events of the southern Levant (Hirsch et al., 1998). Here we trace events on the Gondwanian Tethys platform-shelf during the Jurassic Period and look at the rock formations, fossils (e.g. brachiopods, ammonites, ostracodes) and distribution of these organisms in the southern Levant. The section ends with a discussion of the tectono-eustatic cyclic events and a sequence stratigraphic view of these events.

The last paper is a description of rhynchonellide brachiopods from the Jordan Valley (Feldman, et al., 2012) in which are described seven brachiopod genera including two new species. This fauna was collected from the Mughaniyya Formation of northwest Jordan and inhabited a near shore environment during Jurassic times. The fauna here can be correlated with the faunas of the Aroussiah Formation in northern Sinai and the Zohar and Matmor formations in southern Israel.

REFERENCES

Ager, D.V. 1973. Mesozoic Brachiopoda. In A. Hallam (ed.), *Atlas of Paleobiogeography.* Amsterdam: Elsevier.

Arkell, W.J. 1956. *Jurassic Geology of the World*. Edinburgh: Oliver and Boyd.

------. 1952. Jurassic ammonites from Jebel Tuwayq, Central Arabia. *Philosophical Transactions of the Royal Society of London*, Series B, 236: 241-313.

Avnimelech, M. 1952. Les Mollusques du desert de Judee. *Journal de Conchyliologi*e 92: 77.

Avnimelech, M. 1961a. Pachydiscid ammonite from Campanian chert of Israel. *Israel Research Council Bulletin* 10G: 7-9.

------. 1961b. Isocrinid fragment from upper Galilee of assumed Middle Cretaceous age. *Israel Research Council Bulletin* 10G: 1-4.

Avnimelech, M., A. Parnes, and Z. Reiss. 1954. Molluscs and foraminifera from the Lower Albian of the Negev (Southern Israel). *Journal of Paleontology*, 28: 835-839.

Bartov, Y. 1974. Transverse faults of the central Sinai-Negev fault zone. Abstracts of papers presented at the 1972/1973 seminar of the Geological Survey of Israel, D. Gill (ed.), 11-13.

Bein, A. 1971. Rudistid fringing reefs of Cretaceous shallow carbonate platform of Israel. *American Association of Petroleum Geologists Bulletin* 60: 258-272.

Benjamini, C., F. Hirsch, and Y. Eshet. 2005. The Triassic of Israel. In J. K. Hall, V. A. Krasheninnikov, F. Hirsch, C. Benjamini, and A. Flexer. *Geological Framework of the Levant, Volume II: the Levantine Basin and Israel*, 331-360. Jerusalem: Historical Productions-Hall.

Brett, C. E. 1995. Sequence stratigraphy, biostratigraphy, and taphonomy in Shallow marine environments. *Palaios* 10: 597-616.

-----. 1998. Sequence stratigraphy, paleoecology, and evolution: biotic clues and responses to sea-level fluctuations. *Palaios* 13: 241-262.

Cooper, G. A. 1989. Jurassic brachiopods of Saudi Arabia. *Smithsonian Contributions to Paleobiology* 65: 1-213.

Cossmann, M. 1925. Description des espéces. In H. Douvillé (ed.), Le Callovien dans le massif de Moghara, 305-328, *Bulletin Société Géologique de France*, Sér. 4, 25.

Douvillé, H. 1916. Les Terraines Secondaire dans le massif de Moghara a l'Est de l'Isthme Suez. *Academie de Science Paris, Memoire* 54: 1-184.

------. 1925. Le Callovien dans le massif de Moghara: avec description des fossiles par M. Cossmann. *Bulletin Société Géologique de France*, Sér. 4, 25: 305-328.

Druckman, Y. 1969. The petrography and environment of deposition of the Triassic Saharonim Formation and the Dolomite Member of the Mohilla Formationin Makhtesh Ramon, central Negev (southern Israel). *Geological Survey of Israel Bulletin* 49: 1-22.

------. 1974. Triassic paleogeography of southern Israel and Sinai Peninsula. Symposium, Wien, May 1973. *Schriftenreihe der Erdwissenschaftlichen Kommissionen. Oesterreichische Akademie der Wissenschaften* 2: 79-86.

Dubar, G. 1967. Brachiopodes Jurassiques du Sahara Tunisien. *Annales de Paléontologie* 53: 1-71.

Feldman, H. R. 1987. A new species of the Callovian (Jurassic) brachiopod *Septirhynchia* from northern Sinai. Journal of Paleontology, 61: 1156-1172.

------. 2002. A new species of *Coenothyris* (Brachiopoda) from the Triassic (Upper Anisian-Ladinian) of Israel. *Journal of Paleontology* 76: 34-42.

------. 2005. Paleoecology, taphonomy and biogeography of a *Coenothyris* community (Brachiopoda, Tereratulida) from the Triassic (Upper Anisian-Lower Ladinian) of Israel. *American Museum Novitates* 3479: 1-19.

Feldman, H. R. and C. E. Brett. 1997a. Paleoecology of Jurassic crinoids from Hamakhtesh Hagadol, southern Israel. Israel Geological Society Annual Meeting, 21.

------. 1997b. Epi- and endobiontic organisms on Late Jurassic crinoid columns from the Negev Desert, Israel: Implications for coevolution. Geological Society of America Northeastern Section Meeting, King of Prussia, Pennsylvania 29: 45.

------. 1998. Epi- and endobiontic organisms on Late Jurassic crinoid columns from the Negev Desert, Israel: Implications for coevolution. *Lethaia* 31: 57-71.

Feldman, H. R., F. Hirsch, and E. F. Owen. 1982. A comparison of Jurassic and Devonian brachiopods communities: trophic structure, diversity, substrate relations and niche replacement. Third North American Paleontological Convention Proceedings, Montreal, Canada, 1:169-174. (Reprinted In Y. Bartov [ed.], *Research in Sinai: Collected reprints*, vol. 3, reprint no. 81, April, 1984. *Geological Society of Israel Special Publication* no. 1 and *Journal of Paleontology* 56: 9-10, supplement to no. 2).

Feldman, H. R., and E. F. Owen. 1988. *Goliathyris lewyi*, new species (Brachiopoda, Terebratellacea), from the Jurassic of Gebel El-Minshera, northern Sinai. *American Museum Novitates* 2908: 1-12.

Feldman, H. R., E. F. Owen, and F. Hirsch. 1991. Brachiopods from the Jurassic of Gebel El-Maghara, northern Sinai. *American Museum Novitates* 3006: 1-28.

Feldman, H. R., M. Schemm-Gregory, F. Ahmad, and M. A. Wilson. 2012. Rhynchonellide brachiopods from the Jordan Valley. *Acta Palaeontologica Polonica* 57: 191–204.

Feldman, H. R., V. Radulovic, A. A. Hegab, and B. Radulovic. 2012. Brachiopods from Gebel Engabashi, northern Sinai. *Journal of Paleontology* 86: 238-252.

Freund, R. 1961. Distribution of Lower Turonian ammonites in Israel and neighbouring countries. *Israel Research Council Bulletin* 10G: 79-100.

Freund, R. and M. Raab. 1969. Lower Turonian ammonites from Israel. *Palaeontological Association, Special Paper* 4: 1-83.

Friedman, G. M., Y. Arkin, and E. Aharoni. 1979. Patch of pinnacle reefs of Cretaceous age exposed on western margin of Dead Sea (Israel). *Sedimentology* 26: 143-49.

Gavish, E. 1974. Mineralogy and Geochemistry of a coastal sabkhas near Nabek, Gulf of Eilat. Abstracts of papers presented at the 1972/1973 seminar of the Geological Survey of Israel, D. Gill (ed.), 18-19.

Grader, P. and Z. Reiss (eds.). 1959. *Geological Survey of Israel Summary of Activities*. Geological Survey of Israel, Ministry of Development.

Hildebrand, N. 1974. Structural geology of the Haimur Block, northern Gulf of Elat. Abstracts of papers presented at the 1972/1973 seminar of the Geological Survey of Israel, D. Gill (ed.), 7-9.

Hirsch, F. 1972. Middle Triassic conodonts from Israel, Southern France and Spain. *Mitteilungen Gesellschaft Geologie Bergbaustudenten* 21:811-828.

------. 1976. Sur l'origine des particularisms de la faune du Trias et du Jurassique de la plate-forme African-arabe. *Bulletin Societe Geologique France* 2: 543-552.

------. 1977a. Some conodont-, bivalve-, and gastropod-biostratigraphic results in the Triassic and Jurassic of Israel and adjacent countries. Geological Survey of Israel, Abstracts of papers presented at the 1974-76 seminar: 12-15.

------. 1977b. Note on *Neospathodus* cf. *kockeli* (Tatge) (Conodonta) from Ramon 1 well Central Negev. *Israel Journal of Earth Sciences* 26: 94-96.

-----. 1978. Biological constituents in the Callovian-early Oxfordian (Jurassic) sediments of southern Israel and northern Sinai. 10th International Congress on Sedimentology, Jerusalem, July 1978, Abstracts, 1: 309.

------. 1980. Jurassic bivalves and gastropods from northern Sinai and southern Israel. *Israel Journal of Earth Sciences* 28: 128-163.

Hirsch, F., J.-P. Bassoulett, E. Cariou, B. Conway, H. R. Feldman, L. Grossowicz, A. Honigstein, E. F. Owen, and A. Rosenfeld. 1998. The Jurassic of the southern Levant. Biostratigraphy, palaeogeography and cyclic events. *In* S. Carasquin-Soleau and É. Barrier (eds.), Peri-Tethys memoir 4: epicratonic basins of Peri-Tethyan platforms, *Mémoires du Muséum national d'Histoire Naturelle* 179: 213-135.

Hof, C. H. J. 1998. Late Cretaceous stomatopods (Crustacea, Malacostraca) from Israel and Jordan. *Contributions to Zoology* 67: 257-266.

Kitchin, F. L. 1900. Jurassic Fauna of Cutch, part. 1: The Brachiopoda. *Palaeontologica Indica*, series 3: 1-87.

Lerman, A. 1960. Triassic pelecypods from southern Israel and Sinai. *Israel Research Council Bulletin* 9G: 1-60.

Levy, Y. 1974. Sedimentary reflection of depositional environment in the Baradwil Lagoon, northern Sinai. *Journal of Sedimentary Petrology* 44: 219-227.

Lewy, Z. 1967. Some Late Campanian nostoceratid ammonites from southern Israel. *Israel Journal of Earth Sciences* 16: 165-173.

------. 1969a. Late Campanian heteromorphy ammonites from southern Israel. *Israel Journal of Earth Science*s 18: 109-135.

------. 1969b. Upper Campanian ammonites from the Negev, southern Israel. *Israel Journal of Earth Sciences* 18: 164.

------. 1972. Xenomorphic growth in ostreids. *Lethaia* 5: 347-352.

------. 1973. Pigmentation patterns preserved on late Turonian oysters. *Israel Journal of Earth Science*s 22: 64-65.

------. 1976. Morphology of the shell in Gryphaeidae. *Israel Journal of Earth Sciences* 25: 45-50.

------. 1977. Late Campanian *Pseudoceratites* from Israel and Jordan. *India Palaeontological Society* 20: 244-250.

------. 1981. A Late Albian *Hypengonoceras* (Ammonoidea) from the "Bentonite Bed" at Makhtesh Ramon. *Israel Journal of Earth Sciences* 30: 35-38.

------. 1982. *Gryphaeligmus* n. gen. (Bivalvia: Malleidae) from the Bathonian of the Middle East. *Journal of Paleontology* 56: 811-815.

------. 1985a. Paleoecological significance of Cretaceous bivalve borings from Israel. *Journal of Paleontology* 59: 643-648.

------. 1995. Hypothetical endosymbiotic zooxanthellae in rudists are not need to explain their ecological niches and thick shells in comparison with hermatypic corals. *Cretaceous Research* 16: 25-37.

Lewy, Z., and G. Honig. 1985. A Late Coniacian ammonite from the lower part of The Sayyarim Formation near Elat (southern Israel). *Israel Journal of Earth Sciences*, 34: 205-210.

Lewy, Z., and C. Samtleben. 1979. Functional morphology and Palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia* 12: 341-351.

Marquez-Aliaga, A. and F. Hirsch. 1988. Migration of Middle Triassic bivalves in the Sephardic Province. *Congress Geol. De Espana*, 2nd, Granada, 1: 301-304.

Mishnaevsky, G. 1966. Occurrence of *Ostrea Eilatensis*: A new oyster species from the Cenomanian of Israel and Egypt. *Nature* 210: 517-518.

------. 1967. Some Cenomanian ostreids from Israel. *Israel Journal of Earth Sciences* 16: 132-139.

Muir-Wood, H. M. 1935. Jurassic Brachiopoda. In W. A. Macfadyen et al., *The Geology and Palaeontology of British Somaliland*, 75-147. London: Government of the Somaliland Protectorate.

Neumann, A. C. 1966. Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge *Cliona lampa*. *Limnology and Oceanography* 11: 92-108.

Palmer, T. J. 1982. Cambrian to Cretaceous changes in hardground communities. *Lethaia* 15: 309-323.

Parnes, A. 1958. A Coniacian ammonite from the southern Negev (Israel): *Muniericeras lapparenti grossouvre* var. *Israel Research Council Bulletin* 7G: 167-172.

------. 1961. On the occurrence of *Pseudopygurus* Lambert in southern Israel. *Bulletin of the Research Council of Israel* 10G: 216-222.

------. 1963. The Middle Jurassic fauna of Makhtesh Ramon. *Israel Journal of Earth Sciences* 12: 91.

------. 1964. Coniacian ammonites from the Negev (southern Israel). *Geological Survey of Israel Bulletin* 39: 1-42.

------. 1965. Note on Middle Triassic ammonites from Makhtesh Ramon (southern Israel). *Israel Journal of Earth Sciences* 14: 9-17.

------. 1971. Late Lower Cambrian trilobites from the Timna area and Har Amram, southern Negev, Israel. *Israel Journal of Earth Sciences* 20: 179-205.

------. 1974. Biostratigraphic synchronization of the Middle Jurassic in Makhtesh Ramon, Gebel Maghara and Morocco. Israel Geological Society Annual Meeting, Jerusalem, Abstracts, 14-15.

------. 1975. Middle Triassic ammonite biostratigraphy in Israel. *Geological Survey of Israel Bulletin* 66: 1-35.

------. 1977. On a binodose keeled ceratitid from southeastern Spain (a representative of a line parallel to the genus *Gevanites* Parnes 1975 from the Ladinian of Israel). *Cuadernos Geologic Iberica* 4: 522-525.

------. 1980. Lower Jurassic (Liassic) invertebrates from Makhtesh Ramon (Negev, southern Israel). *Israel Journal of Earth Sciences* 29: 107-113.

------. 1981. Biostratigraphy of the Mahmal Formation (Middle and Upper Bajocian) in Makhtesh Ramon (Negev, southern Israel). *Geological Survey of Israel Bulletin* 74: 1-55.

------. 1986. Middle Triassic cephalopods from the Negev (Israel) and Sinai (Egypt), with an introduction on the Triassic in Israel by I. Zak. *Geological Survey of Israel Bulletin* 79: 9-59.

Parnes, A., C. Benjamini, and F. Hirsch. 1985. New aspects of Triassic ammonoid biostratigraphy, paleoenvironment and paleobiogeograpy in southern Israel (Sephardic Province). *Journal of Paleontology* 59: 656-666.

Picard, L., and A. Flexer. 1974. *Studies on the stratigraphy of Israel: the Triassic*. Tel Aviv: Israel Institute of Petroleum.

Raab, M. 1962. Jurassic-Early Cretaceous ammonites from the southern coastal plain, Israel. G*eological Survey of Israel Bulletin* 34: 24-30.

Raup, D. M., and S. M. Stanley. 1978. *Principles of Paleontology*. New York: W. H. Freeman & Co.

Reiner, W. 1968. Callovian gastropods from Hamakhtesh Hagadol (southern Israel). *Israel Journal of Earth Sciences* 17: 171-198.

Remy, J. M., and M. Avnimelech. 1955. *Eryon yehoachi* n. sp. et gen. *Cenomanocarcinus* cf. *Vanstraeleni stenzel* crustaces decapodes du Cretace Superieur de L'Etat D'Israel. *Bulletin de la Société Géologique de France* 5: 311-314.

Sepkoski, J. J., Jr. 1978. A kinetic model of Phanerozoic taxonomic diversity. I. Analysis of marine orders. *Paleobiology* 4: 223-251.

Shaw, A. B. 1964. *Time in Stratigraphy*. New York: McGraw-Hill Book Co.

Shaw, S. H. 1947. *Southern Palestine, geological map* on a scale of 1:250,000 with explanatory notes. Jerusalem: Government of Palestine.

Shimron, A. 1974. The metamorphic rocks of the Sinai Peninsula. Abstracts of papers presented at the 1972/1973 seminar of the Geological Survey of Israel, D. Gill (ed.), p 3.

Shi, X., and R. E. Grant. 1993. Jurassic rhynchonellids: internal structures and taxonomic revisions. *Smithsonian Contributions to Paleobiology* 73: 1-190.

Shirav, M. 1974. Stratigraphy and structure, the Quseib Graben, northern Gulf of Elat. Abstracts of papers presented at the 1972/1973 seminar of the Geological Survey of Israel, D. Gill (ed.), p 4-6.

Stanley, S. M., and L. A. Hardie. 1998. Secular oscillations in the carbonate mineralogy of reef-building and sediment-producing organism driven by tectonically forced shifts in seawater chemistry. *Palaeogeography, Palaeoclimatology, Palaeoecology* 144: 3-19.

Taylor, P. D., and M. A. Wilson. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews* 62: 1-103.

Vermeij, G.J. 1977. The Mesozoic marine revolution; evidence from snails, predators and grazers. *Paleobiology* 3: 245-258.

------. 1987. *Evolution and Escalation: An Ecological History of Life.* Princeton: Princeton University Press.

Weir, J. 1925. Brachiopoda, Lamellibranchiata, Gastropoda and Belemnites, pp. 79-110. In The Collection of Fossils and Rocks from Somaliland made by Messrs. B. K. N. Wyllie and W. R. Smellie. *Monographs of the Geological Department of the Hunterian Museum, Glasgow University* 1: 1-180.

------. 1929. Jurassic Fossils from Jubaland, East Africa, Collected by V. G. Glenday. *Monographs of the Geological Department of the Hunterian Museum, Glasgow University* 3: 1-63.

Weisbrod, T. 1969. The Paleozoic of Israel and adjacent countries, part I: the subsurface Paleozoic stratigraphy of southern Israel. *Geological Survey of Israel Bulletin* 47: 1-35.

------. 1976. The Permian in the Near East. In Falke, H. (editor), *The Continental Permian in Central, West and South Europe. NATO Advanced Study Institute Series* 22: 200-214. Dordrecht, Holland: D. Reidel Publishing Group.

Wilson, M. A., H. R. Feldman, and E. B. Krivicich. 2010. Bioerosion in an equatorial Middle Jurassic coral-sponge reef community (Callovian, Matmor Formation, southern Israel). *Palaeogeography, Palaeoclimatology, Palaeoecology* 289: 93-101.

Wilson, M. A., H. R. Feldman, J. C. Bowen, and Y. Avni. 2008. A new equatorial, very shallow marine sclerozoan fauna from the Middle Jurassic (Late-Callovian) of southern Israel. *Palaeogeography, Palaeoclimatology, Palaeoecology* 263: 24-29.

Zak, I. 1963. Remarks on the stratigraphy and tectonics of the Triassic of Makhtesh Ramon. *Israel Journal of Earth Sciences* 12: 87-89.

ACKNOWLEDGMENTS

I am particularly indebted to my brilliant mentor, Dr. Arthur J. Boucot, Oregon State University, who steered me into the fascinating world of brachiopod paleontology. He provided the inspiration for my lifelong study of the Brachiopoda and was the driving force behind my love of research. Art emphasized that taxonomy is critical to progress in our field since it serves as the basis for studies in evolution, paleoecology and biogeography. I thank my professor and advisor at Rutgers University, Dr. Richard K. Olsson, who constantly challenged me with thought provoking questions. I am grateful to Dr. Niles Eldredge, the American Museum of Natural History (AMNH), for arranging my appointment as research associate in the Division of Paleontology (Invertebrates) and his constant support over the years, and Dr. Neil Landman (AMNH), for his discussions on paleoecology and cladistics. I thank the late Dr. Stephen Jay Gould, Harvard University, for general discussions on paleontology when I first began my career. I benefitted from numerous conversations, discussions and exchange of ideas from Drs. Mena Schemm-Gregory, University of Coimbra (deceased) and Mark A. Wilson, the College of Wooster. Many thanks are due to Susan Klofak and Stephen Thurston (AMNH) for specimen preparation and photographic work. Mai Reitmeyer, Research Services Librarian (AMNH), was particularly helpful to me in locating obscure references on the Mesozoic paleontology of the Middle East.

I thank Dr. Simcha Fishbane, Touro College and University System (TCUS), who first suggested putting this volume together and Dr. Michael Shmidman (TCUS), for his advice in its preparation. I thank Dr. Alan Kadish, President of the Touro College and University System, for his support and encouragement in preparing this volume. I am grateful to deans Stanley L. Boylan and Anthony Polemeni, Touro College, for providing funding from the Faculty Development Fund that enabled me to present the results of my research at various scientific venues. I acknowledge the Touro College Faculty Research Fund for supporting my field work and thank the members of its peer review panel.

My colleagues at the Geological Survey of Israel (GSI) provided field support, laboratory space, access to the library as well as critical comments and discussions over many field seasons. I am especially grateful to Drs. Francis Hirsch, Zeev Lewy and the late Abraham Parnes (GSI). Mr. Moshe Arnon (GSI) served as technician on my first trip to the Sinai Peninsula and was instrumental in making the field excursion run smoothly.

I thank my editors at Academic Press, Sharona Vedol and Deva Jasheway for critically reading the manuscript and making helpful suggestions for improvement.

It should be noted that a variety of traditional Jewish authorities and texts have dealt with the particular issues concerning the age of the universe, and have offered diverse approaches for resolving any apparent conflicts that might arise between Jewish tradition and modern science on this matter.[1] This author follows the lead of these traditional authorities in operating with the accepted principles of the science of paleontology.

[1] See, e.g., Babylonian Talmud, standard editions, Hagigah 13b; Midrash Bereshit Rabba, ed. J. Theodor and C. Albeck (Jerusalem, 1996), 3, 5; Rabbi Isaac of Akko, Ozar ha-Hayyim, Ms. Moscow-Russian State Library, Guenzburg 775, 86b-87b ; Rabbi Yisrael Lifshitz, Derush Or Ha-Hayyim, in his Tiferet Yisrael on Mishnah, end of Nezikin (Danzig, 1845), 276b-279b.

A COMPARISON OF JURASSIC AND DEVONIAN BRACHIOPOD COMMUNITIES: TROPHIC STRUCTURE, DIVERSITY, SUBSTRATE RELATIONS AND NICHE REPLACEMENT

ABSTRACT

Four Jurassic (Bathonian-Callovian) brachiopod communities from Gebel El-Maghara, northern Sinai, are compared to four Devonian (Eifelian) brachiopod communities from New York. All communities recognized were examined in terms of composition, trophic structure, diversity, and relation to substrate. Conclusions reached regarding the Jurassic communities pertain only to local areas in northern Sinai and are strictly local observations. The faunas of the Jurassic communities show a close affinity with Eurasian Tethyan shelf faunas and, situated on the African continent, form an important link between the European faunas and those of Afro-Indian origin.

INTRODUCTION

During the past decade, paleobiologists have increasingly focused on trophic structure as a means of reconstructing ancient communities. One of the trends in recent years has been to compare paleocommunities and living communities (a paleocommunity is defined as a suite of preservable taxa comprising a community, as opposed to a living community, which consists of all taxa in the community, *sensu* Scott and West, 1976). In this preliminary study we compare four Devonian brachiopod communities to four Jurassic brachiopod communities and evaluate trophic structure, diversity, and substrate relations in order to assess and recognize any major trends from the mid-Paleozoic to mid-Jurassic.

The non-reef paleocommunities of the Onondaga Limestone (Devonian, Eifelian) in New York have been analyzed by Feldman (1980) and Lindemann and Feldman (1981) with respect to distribution, diversity, functional morphology, and substrate relations, but trophic structure was not studied in detail. A paper on the systematics of the Onondagan brachiopods (Feldman, 1980) includes additional distributional data and collecting localities.

The Middle Jurassic section at Gebel El-Maghara, northern Sinai, which was sampled in this study is over 600 meters thick. The brachiopod, molluscan, and echinoderm faunas were described by Douvillé (1916) but no one has studied the brachiopods in detail since Cossmann (in Douvillé, 1925) studied the Callovian bivalves and gastropods of Sinai and Hirsch (1979) and reported on the bivalves and gastropods of northern Sinai and southern Israel.

The brachiopod faunas of northern Sinai are significant in that they show a close affinity with Eurasian Tethyan shelf faunas and, situated on the African continent, form a key link between European faunas and those of Afro-Indian origin. Based upon data collected, we suspect that the Ethiopian Province (i.e., northern Sinai) was invaded by brachiopods migrating from the north in early Jurassic times which were isolated for the remainder of the Jurassic. These faunas are thought to have subsequently developed special morphological features which distinguish them from their original stock. A detailed systematic study of the Brachiopods is in preparation (Feldman, Owen and Hirsch) which will yield functional morphological data as well as result in a revision of those genera and species described before Muir-Wood (1934, 1935) and which lack internal descriptions.

TROPHIC ANALYSIS OF SPECIFIC COMMUNITIES

Atrypa-Coelospira-Nucleospira Community.—This community is found in mudstones and wackestones of the Onondaga Limestone (Devonian, Eifelian) in the Mid-Hudson Valley, southeastern New York. The environment of deposition was most likely mid-neritic with a moderately to highly agrillaceous lime mud or lime sand substrate (Feldman, 1980). Of the four Devonian communities studied, the *Atrypa-Coelospira-Nucleospira* Community shows the greatest diversity. Six major taxa were recovered (Table 1): Brachiopods (32 species), corals (13 genera), gastropods (4 species), echinoderms (indetermined number of crinoid species), trilobites (1 species) and bryozoans (2 species). The trophic nucleus of the community is composed mainly of spiriferid brachiopods, low-level suspension feeders. Note that the brachiopods show the greatest diversity in the community. The next most abundant group is the corals (high-level suspension feeders) followed by the gastropods (collectors? browsers? scavengers?), echinoderms (crinoids, passive high-level suspension feeders), trilobites (semi-infaunal burrowers? collectors? scavengers? predators?) and bryozoans (low-level and high-level suspension feeders). The *Atrypa-Coelospira-Nucleospira* Community shows excellent structure and stratification with regard to trophic levels. The high diversity appears to be indicative of a low stress environment. (See table 1)

TABLE 1: Trophic structure and diversity of the *Atrypa-Coelospira-Nucleospira* Community.

Major Taxon (in order of relative abundance)	General Morphology	Trophic Group
Brachiopods	Varied,* but predominantly dorsibiconvex, cancavo-convex, plano-convex, and biconvex spiriferids	Low-level suspension feeders
Corals	Solitary and colonial	High-level suspension feeders
Gastropods	Spinose platyceratids	Collectors? browsers? scavengers?
Echinoderms	Non-pinnulate inadunate crinoids ossicles	Passive high-level suspension feeders
Trilobites	Fragments with inflated glabellas (Phacopids?)	Semi-infaunal burrowers? collectors? scavengers? predators?
Bryozoans	Encrusting and ramose fragments	Low-level and high-level suspension feeders.

* A total of 32 species have been recovered, 17 of which are spiriferids.

Atrypa-Megakozlowskiella Community.—This community occurs in the mudstones and wackestones of the Onondaga Limestone from Cherry Valley to Clarkesville, New York. The environment of deposition was mid-neritic with a moderately argillaceous lime mud or lime sand substrate (Feldman, 1980). Diversity (Table 2) is greatest among the brachiopods (22 species), low-level suspension feeders, followed by the corals (high-level suspension feeders), echinoderms (crinoids, passive high-level suspension feeders), trilobites (semi-infaunal burrowers? collectors? scavengers? predators?), bryozoans (high-level suspension feeders), and gastropods (collectors? browsers? scavengers?). The trophic nucleus is composed mainly of spiriferid brachiopods. Here, as in the *Atrypa-Coelospira-Nucleospira* Community, there is excellent stratification of trophic levels with eight different trophic groups recognized. The high diversity appears to be indicative of a low stress environment. (See table 2).

TABLE 2: Trophic structure and diversity of the *Atrypa-Megakozlowskiella* Community.

Major Taxon (in order of relative abundance)	General Morphology	Trophic Group
Brachiopods	Varied,* but predominantly dorsibiconvex and ventribiconvex spiriferids	Low-level suspension feeders
Corals	Solitary and colonial	High-level suspension feeders
Echinoderms	Non-pinnulate inadunate crinoids ossicles	Passive high-level suspension feeders
Trilobites	Indet. Fragments (molts?)	Semi-infaunal burrowers? collectors? scavengers? predators?
Bryozoans	Trepostome? fragments	High-level? suspension feeders
Gastropods	Lenticular tropidodiscids	Collectors? browsers? scavengers?

* A total of 32 species have been recovered, 11 of which are spiriferids.

Leptaena-Megakozlowskiella Community.—This community is found in mudstones and wackestones of the Onondaga Limestone in central New York, in the vicinity of Syracuse. The environment of deposition was probably mid-neritic with a moderately to highly argillaceous lime mud or lime sand substrate (Feldman, 1980). Brachiopods (low-level suspension feeders) comprise the trophic nucleus (Table 3) with 17 species followed by corals (high-level suspension feeders), echinoderms (crinoids, passive high-level suspension feeders), trilobites (semi-infaunal burrowers? collectors? scavengers? predators?), gastropods (collectors? browsers? scavengers?), bryozoans (high-level suspension feeders) and cephalopods (predators). Again, eight different trophic groups are recognized, minimizing feeding competition in this highly stratified community. As in the two previous communities discussed, high diversity here appears to indicate a low stress environment. (See table 3)

Table 3: Trophic structure and diversity of the *Leptaena-Megakozlowskiella* Community.

Major Taxon (in order of relative abundance)	General Morphology	Trophic Group
Brachiopods	Varied,* but predominantly concavoconvex strophomenids and ventribiconvex spiriferids	Low-level suspension feeders
Corals	Solitary and colonial	High-level suspension feeders
Echinoderms	Camerate crinoid columnals	Passive high-level suspension feeders
Trilobites	Medium sized flat forms with spine-bearing pygidia, pear-shaped and inflated glabellas	Semi-infaunal burrowers? collectors? scavengers? predators?
Gastropods	Lenticular, trochiform, and discoid morphotypes	Collectors? browsers? scavengers?
Bryozoans	Ramose fragments	High-level suspension feeders
Cephalopods	Subdiscoid and lenticular morphotypes	Predators

* A total of 17 species have been recovered, 8 of which are spiriferids.

Amphigenia? Community.—This community occurs in a sandstone facies of the Onondaga Limestone in central New York. The environment of deposition was inner-neritic with a sand substrate (Feldman, 1980). Of all the Devonian communities studied, the *Amphigenia*? Community shows the least diversity (Table 4). Although only two major taxa are found in this community, they are stratified such that they feed at different trophic levels: brachiopods (low-level suspension feeders) and corals (high-level suspension feeders). The low diversity and coarse substrate are indicative of a high stress environment.

Table 4: Trophic structure and diversity of the *Amphigenia*? Community.

Major Taxon (in order of relative abundance)	General Morphology	Trophic Group
Brachiopods	Robust biconvex terebratulids	Low-level suspension feeders
Corals	Solitary and colonial	High-level suspension feeders

Eudesia Community.—The *Eudesia* Community (Jurassic, Upper Bathonian) is found in interbedded, in places microoncolithic, friable limestones and thin-bedded calcareous shales of the Sherif Formation, Gebel El-Maghara, northern Sinai. The general environment of deposition of the Sherif Formation in southern Israel and northern Sinai was a peritidal shelf environment indicative of alternating sequences of clastics and carbonates, representative of continually shifting river systems which drained the Arabo-Nubian shield (Goldberg and Friedman, 1974). However, locally, the environment of deposition appears to have been one of low-energy (mid-neritic) with a low rate of deposition, dominated by brachiopods and bivalves (*Eligmus, Africogryphaea*, and *Gryphaeligmus*) on a mud substrate. Brachiopod diversity is markedly reduced from the Devonian communities. In the *Eudesia* Community (Table 5) only 1 brachiopod genus (i.e. *Eudesia*) represents the trophic nucleus. There is present, however, an additional rare species of smooth terebratulid. The brachiopods (low-level suspension feeders) are closely followed in abundance by bivalves (low-level suspension feeders), rare gastropods (collectors? browsers? scavengers?) rare cephalopods (predators), and rare echinoderms (scavengers, predators). Structure and stratification of trophic levels is not as good as in the first three Devonian communities discussed above, and only five different trophic groups are recognized here. The relatively high diversity appears to indicate a low stress environment, although the presence of bivalves in the number 2 biovolume dominance position may indicate a position closer to the shore. (See table 5)

Table 5: Trophic structure and diversity of the *Eudesia* Community.

Major Taxon (in order of relative abundance)	General Morphology	Trophic Group
Brachiopods	Biconvex multiplicate and rare smooth terebratulids	Low-level suspension feeders
Bivalves	Ostreids, malleids	Low-level suspension feeders
Gastropods	Medium-spired morphotypes	Collectors? browsers? scavengers?
Cephalopods	Oxyconic ammonites	Predators
Echinoderms	Regular echinoids	Scavengers, predators

Ptychtothyris Community.—This community occurs in the upper part of the Sherif Formation (upper Bathonian), Gebel El-Maghara, in a shallower marine environment than the underlying *Eudesia* Community. The shale content is greater and microoncolites are present along with recrystalized limestone due to aragonite dissolution of shallow marine organisms (Z. Lewy, personal communication). Here again brachiopod diversity is reduced from that of the Devonian. The trophic nucleus (Table 6) consists of brachiopods (over 95% *Ptychtothyris,* 3% *Eudesia*, 2% indet. sp.) (low-level suspension feeders) followed in abundance by bivalves (low-level suspension feeders), gastropods (collectors? browsers? scavengers?), and echinoderms (scavengers, predators). A mid-neritic environment of deposition is assigned, although the presence of microoncolites would seem to indicate a higher energy environment. Trophic structure and stratification are similar to that of the *Eudesia* Community with only four different trophic groups recognized. Bivalves are again in the number 2 biovolume dominance position.

Certain parameters typical of opportunistic species (see Levinton, 1970; Alexander, 1977) appear to be applicable to the genus *Ptychtothyris.* Although found in adjacent strata, *Ptychtothyris* reaches overwhelming numerical abundance (95%) in some strata. There is a definite lack of size sorting within the population. The cause of this possible opportunistic explosion is not certain. It may have been related to substrate mobility and/or reduced salinity caused by the drainage of river systems from the adjacent Arabo-Nubian shield. Goldberg and Friedman (1974) report that the presence of clastic rocks within the Sherif Formation suggests runoff of sand- and mud-bearing river water from nearby land areas. (See table 6)

Table 6: Trophic structure and diversity of the *Ptychtothyri*s Community.

Major Taxon (in order of relative abundance)	General Morphology	Trophic Group
Brachiopods	Smooth and multiplicate biconvex terebratulids	Low-level suspension feeders
Bivalves	Ostreids	Low-level suspension feeders
Gastropods	Medium-sized, medium-spired morphotypes	Collectors? browsers? scavengers?
Echinoderms	Regular echinoids, medium-spired morphotypes	Scavengers, predators

Septirhynchia Community.—The *Septirhynchia* Community (Lower Callovian?) is found in the Zohar Formation, Gebel El-Maghara, just above a series of crumbly limestones in a hard, dense, buff colored limestone with a distinct chert band at the top. The lowermost meter contains the entire fauna which is biostromal in some parts. The environment of deposition appears to have been mid-neritic. The trophic nucleus (Table 7) consists of brachiopods (over 99% *Septirhynchia*) (low-level suspension feeders), followed in abundance by bivalves (low-level suspension feeders), corals (high-level suspension feeders) and gastropods (collectors? browsers? scavengers?). No ammonites have been found associated with this community. Stratification is not well developed here, although the large size of the brachiopods may in actuality bring them into direct competition with the corals in terms of utilization of food resources. Mancenido and Walley (1979) have proposed a life position for *Septirhynchia* which would have placed the anterior commissure of gibbous forms at a level several centimeters above the sediment-water interface. With the commissure vertically oriented, the brachiopod attained a certain amount of stability on the sea floor. Juvenile forms, however, were true low-level suspension feeders since they lived attached by a pedicle accompanied by incurvature of the umbos which was typical of all gibbous forms observed in the field. Although corals are common throughout the outcrops studied, no reef mounds are present. (See table 7)

Table 7: Trophic structure and diversity of the *Septirhynchia* Community.

Major Taxon (in order of relative abundance)	General Morphology	Trophic Group
Brachiopods	Large, strongly costate rhynchonellids and very rare smooth terebratulids, e.g. *Ptychtothyris*	Low-level suspension feeders
Bivalves	Small, inequivalved exogyrids, and subequivalve, irregular ovate malleids	Low-level suspension feeders
Corals	Indet. ramose fragments	High-level suspension feeders
Gastropods	Medium-large sized, medium-spired morphotypes	Collectors? browsers? scavengers?

Somalirhynchia Community.—This community (Upper Callovian) occurs at the top of the Zohar Formation, Gebel El-Maghara, in a yellow, nodular, argillaceous limestone. The environment of deposition was midneritic. The trophic nucleus consists of brachiopods (low-level suspension feeders) followed in abundance by ammonites and belemnites (predators), bivalves (low-level suspension feeders), and gastropods (collectors? browsers? scavengers?). Stratification of trophic levels is fair in this community (Table 8), with five different trophic groups present. Additional data are needed before a further detailed evaluation of this community can be completed. (See table 8)

Table 8: Structure and diversity of the *Somalirhynchia* Community.

Major Taxon (in order of relative abundance)	General Morphology	Trophic Group
Brachiopods	Medium-large sized rhynchonellids, smooth terebratulids.	Low-level suspension feeders
Cephalopods	Ammonites: *Sowerbyceras* with acutely sigmoid constrictions on test; Involute ornate oppeliids, evolute, compressed unicarinate and pachyceratid morphotypes. Belemnite fragments; *Paracenoceras*.	Predators
Bivalves	Ostreids, pectenids	Low-level suspension feeders
Gastropods	Low-, medium-, and high-spired morphotype.	Collectors? browsers? scavengers?

DISCUSSION

Although this study deals with brachiopod communities of the Devonian and Jurassic, additional observations were made pertaining to other marine communities, especially in the Jurassic. These observations are incorporated into the discussion below. The bivalves in the Jurassic, in some cases, may have taken over the ecological niche of the Paleozoic brachiopods subsequent to the Permian crisis. We concur with Gould and Calloway (1980) that after the Permo-Triassic extinction (which affected brachiopods profoundly but clams relatively little) the clams may have been the first back after a brachiopod debacle in which clams played no causal role. They did not actively displace the brachiopods during the Permian crisis. In general, in the Jurassic, we find little evidence for a "takeover" by bivalves and often meet with distinct faunal groups of one phylum or another. It is important to note that conclusions reached here based upon data collected in the Jurassic of northern Sinai, especially regarding niche-replacement, pertain only to local areas and are strictly local observations. Further study will yield additional data which will allow more general conclusions to be drawn regarding Jurassic marine communities.

Table 9 summarizes the niche replacement and biovolume dominance of the eight communities studied. The Devonian and Jurassic communities are similar in that they are all dominated by low-level suspension feeders. However, in the vast majority of the Jurassic communities observed that were not dominated by brachiopods, bivalves invariably moved into the number 1 biovolume dominance position. Thus, the ecological niche representative of the number 1 biovolume dominance position, that is, low-level suspension feeders, was the same in both the Devonian and Jurassic. In the Devonian high-level suspension feeders (corals) were consistently in the number 2 biovolume dominance position but by Jurassic time they dropped to number 5 position. The passive high-level suspension feeders of the Devonian communities do not appear in any of the Jurassic communities. The number 3 biovolume dominance position that they had occupied in the Devonian was taken over by the predators (cephalopods) in the Jurassic. It is noteworthy that the Devonian predators (i.e. cephalopods) occupied a number 7 position indicating their increased importance as Jurassic community faunal constituents. The Devonian trilobites have no exact ecological counterpart in the Jurassic communities we observed, although a crustacean has been reported from the *Eudesia* beds (Z. Lewy, personal communication). Their extinction by the end of the Permian resulted in a vacant niche which may have been taken over, at least in part, by the echinoids. The gastropods maintained a relatively stable ecological position from Devonian through Jurassic, moving from a number 5 to number 4 biovolume dominance position. (See table 9)

Table 9: Niche replacement and dominance in Devonian and Jurassic brachiopod communities.

Period of occurrence and communities	BIOVOLUME DOMINANCE POSITION						
	1	2	3	4	5	6	7
Jurassic 1) *Eudesia* 2) *Ptychtothyris* 3) *Septirhynchia* 4) *Somalirhynchia*	Brachiopods (LLSF)*	Bivalves (LLSF)	Cephalopods (P)	Gastropods (C, B, S)	Corals (HLSF)	Echinoids (P, S)	—
Devonian 1) *Atrypa-Coelospira-Nucleospira* 2) *Atrypa Megakozlowskiella* 3) *Leptaena-Megakozlowskiella* 4) *Amphigenia*?	Brachiopods (LLSF)	Corals (HLSF)	Crinoids (PHLSF)	Trilobites (SB, C, S, P)	Gastropods (C, B, S)	Bryozoans (HL, LLSF)	Cephalopods (P)

* Note that the non-brachiopod dominated marine communities observed in the Jurassic of Gebel El-Maghara, not studied in detail in this report, consistently had mollusks (usually bivalves) in the number 1 biovolume dominance position. Abbreviations: LLSF = low-level suspension feeder; HLSF = high-level suspension feeder; PHLSF = passive high-level suspension feeder; P = predator; C = collector; B = browser; S = scavenger; SB = semi-infaunal burrower.

Turpaeva's (1957) well-known generalizations regarding arctic and boreal marine communities apply to three of the four Devonian communities in that they are: 1) Dominated by one trophic group (low-level suspension feeders) and, 2) Structured such that the second most dominant species belongs to a different trophic group from the most dominant species. However,