Paleoecology, Taphonomy, and Biogeography of a Coenothyris Community (Brachiopoda, Terebratulida) from the Triassic (Upper Anisian–Lower Ladinian) of Israel

Author: FELDMAN, HOWARD R.

Source: American Museum Novitates, 2005(3479) : 1-20

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2005)479[0001:PTABOA]2.0.CO;2

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/American-Museum-Novitates on 09 Apr 2025
Terms of Use: https://bioone.org/terms-of-use

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3479, 19 pp., 7 figures, 4 tables July 25, 2005

Paleoecology, Taphonomy, and Biogeography of a *Coenothyris* Community (Brachiopoda, Terebratulida) from the Triassic (Upper Anisian–Lower Ladinian) of Israel

HOWARD R. FELDMAN[1]

ABSTRACT

A brachiopod community from the Fossiliferous Limestone Member (Upper Anisian–Lower Ladinian) of the Triassic Saharonim Formation at Har Gevanim, Makhtesh Ramon, southern Israel, is dominated by the terebratulid *Coenothyris oweni* Feldman. The community shows evidence of time-averaging and is largely composed of a single cohort of juvenile mortality of one spatfall. The Saharonim Formation was deposited under normal, calm, relatively shallow marine conditions as part of the global Anisian–Ladinian transgression. One horizon, varying in thickness between 1 and 1.5 cm, represents an autochthonous obrution deposit of juvenile *Coenothyris* brachiopods and 10 bivalve genera that were rapidly buried by pulses of clay in the form of flocculated mud. Other faunal constituents of the Saharonim Formation include conodonts, ostracodes, foraminiferans, bivalves, cephalopods, gastropods, echinoderms, and vertebrate remains that belong to the Sephardic Province and are diagnostic of the Middle Triassic series of Israel. The faunal composition and shallow depositional environment of the strata studied are useful in correlating the Triassic rocks in the Negev with those in Europe and help to differentiate the Sephardic Province from the Germanic Muschelkalk and the Alpine Tethyan faunas to the north.

INTRODUCTION

Triassic rocks were first recognized in the Middle East as a result of the discovery of Carnian fossils in 1915 near Latakia in Syria (Picard and Flexer, 1974). Cox (1924) described a Triassic fauna from Transjordan collected by the Turkish Petroleum Company, Awad (1946) wrote on the occurrence of

---

[1] Biology Department, Touro College, New York, NY 10016-7304 (feldspar4@optonline.net).

ISSN 0003-0082

Marine Triassic (Muschelkalk) deposits in the Sinai and Negev (Gebel Areif en-Naqa) deserts, and Shaw (1947) summarized the research done by the British Petroleum Company in southern Israel during World War II. In general, research on the Triassic rocks and fossils in the countries of the Levant was made available after the war when oil companies and governments published the results of their field surveys and wildcat drillings (Picard and Flexer, 1974). Outcrops of Triassic rocks can be found in southern Israel (Makhtesh Ramon; described by Druckman, 1969, 1974a, 1974b, 1976; Zak, 1957), Egypt (Har Arif, Gebel Areif en-Naqa; Parnes, 1986), and in Jordan (Wadi Husban, Wadi Zarka, and Zarka Ma'in; Parnes, 1986). Numerous boreholes in Israel, Sinai, and Jordan (Druckman, 1974a, 1976; Parnes, 1986: fig. 1) have yielded records of Triassic rocks (Bartov et al., 1980; Bender, 1968; Bentor et al., 1965; Druckman, 1974a, 1974b, 1976; Garfunkel and Derin, 1985; Zak, 1957, 1963, 1964).

Based on borehole data and surface outcrops, the thickness of the Triassic rocks in Israel ranges from 500 to 1100 m (Druckman, 1974a). The stratigraphic section is divided into the Negev Group (Yamin and Zafir formations; Weisbrod, 1969, 1976) and Ramon Group (Ra'af, Gevanim, Saharonim, and Mohilla formations; Zak, 1963). The section consists of carbonates, sulfates, sandstones, siltstones, and clays; it is largely clastic in the lower part, more carbonate-rich in the middle, and more evaporitic in the upper part (Druckman, 1969, 1974a, 1976) and ranges in age from Scythian (Early Triassic) to Carnian–Norian (Late Triassic).

The material described in this paper was collected at Har Gevanim in Makhtesh Ramon (N30°35′, W34°55′), a large (40 km long, 8 km wide), northeast-trending structure described by Picard (1951) as a complex erosion funnel, part of the Ramon anticline, in southern Israel (fig. 1). Above the Triassic sediments exposed in the study area, there are Jurassic–Cretaceous beds that cover large parts of the interior of Makhtesh Ramon, as well as alkaline trachybasaltic to trachysyenitic dikes and sills and larger intrusive bodies such as an essexitic laccolith and nordmarkite boss (a plutonic body having an areal extent of less than 40 square miles and a roughly circular outline in map view) (Mazor, 1955; Picard and Flexer, 1974). The shells were recovered from the Fossiliferous (lower) Member of the Saharonim Formation (Upper Anisian–Lower Ladinian) at Har Gevanim, Makhtesh Ramon, southern Israel (fig. 2). The Fossiliferous Member consists of fossiliferous limestone beds alternating with calcareous shales.

This study is an outgrowth of the author's long-term project in the taxonomy, biogeography, and paleoecology of Triassic and Jurassic faunas, particularly brachiopods, in the Middle East (Feldman et al., 1982, 1991; Feldman, 1986, 1987, 2002; Feldman and Owen, 1988, 1993; Feldman and Brett, 1998; Hirsch et al., 1998). Endemic faunas of the Jurassic Ethiopian provinces have been under investigation for many years, and now the Triassic brachiopods of the Negev, belonging to the Sephardic Province, are being revised in order to establish the early history of various brachiopod species and their evolution within the province.

ABBREVIATIONS

AMNH, Division of Paleontology, American Museum of Natural History; GSI, Geological Survey of Israel, Jerusalem; NHM, Department of Palaeontology, Natural History Museum, London.

PALEOECOLOGY AND TAPHONOMY

A *Coenothyris* brachiopod community from the Middle Triassic (Upper Anisian–Lower Ladinian) of southern Israel was collected from the lower part of subunit 31 (Druckman, 1969; 1974), Saharonim Formation, Makhtesh Ramon. This community (hereafter referred to as the *Coenothyis* Bed) is unique in that:

1. It comprises solely juveniles; no ephebic specimens occur in the population, whereas in stratigraphic horizons above and below (subunits 12–15, the top of subunit 31, and subunit 42) there are normal ontogenetic gradations of the brachiopods ranging from neanic to gerontic forms.
2. It represents an obrution deposit which, according to Taylor and Brett (1996), are some of the most common *Lagerstätten* that re-

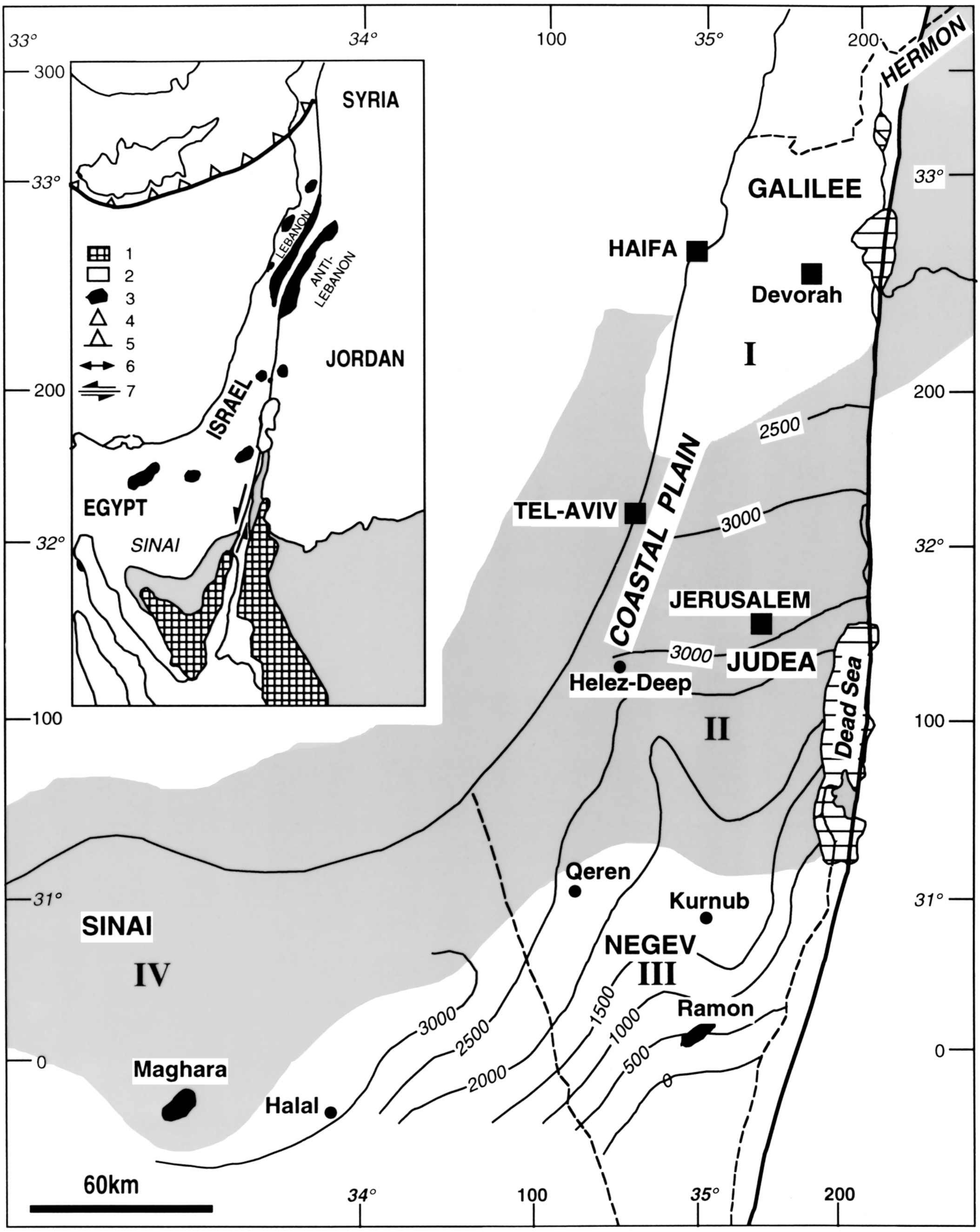

Fig. 1. Location map of Precambrian–Oxfordian exposures in the Levant. 1, Precambrian; 2, Paleozoic–Triassic; 3, Jurassic; 4, Mount Hermon; 5, Alpine thrust-front; 6, 7, Neogene sinistral transform; I, Galilee High; II, Judean Embayment; III, Negev High; IV, Sinai Deep; with extension of Lower Oxfordian Majdal Shams shales (shaded area) and Jurassic isopachs (from Hirsch et al., 1998). ‘‘Ramon’’ signifies the Triassic Ramon Group, an anticlinorium that was breached through several phases of erosion, beginning in the Late Tertiary (Miocene–Pliocene), resulting in erosional cirques (Parnes, 1986). Tectonic movements since the Late Mesozoic, including reactivation of faults, resulted in the development of WSW–ENE- to S–N-trending reverse and thrust faults that today consist of several secondary monoclinal and domal buckles with an associated fault system (Zak, 1963).

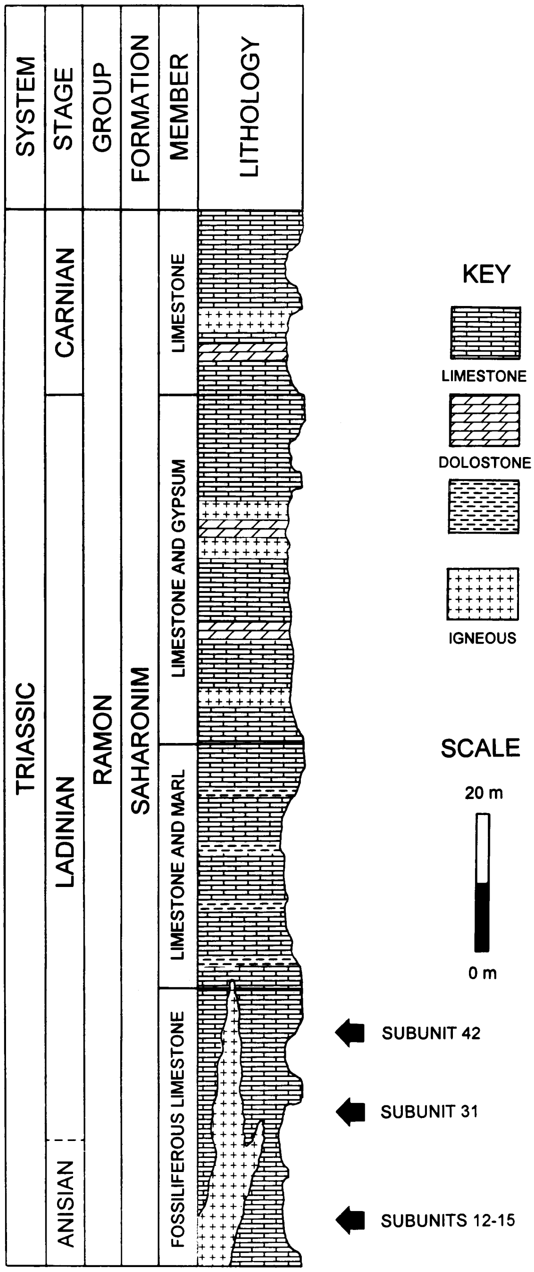

Fig. 2. Generalized columnar section of the Triassic Saharonim Formation at Har Gevanim, Makhtesh Ramon, southern Israel. For detailed stratigraphy, see Druckman (1974b). Arrows represent occurrences of *Coenothyris oweni* Feldman at marked subunit intervals. Subunit designations are after Zak (1964) *in* Parnes (1975).

TABLE 1

Faunal Constituents of the *Coenothyris oweni* Community, Saharonim Formation (Upper Anisian–Lower Ladinian), Makhtesh Ramon, Southern Israel

Taxon	Number	% Composition
Brachiopods		
Coenothyris oweni Feldman	2399	81.54
Bivalves		
Myophoria germanica (Hohenstein)**	72	2.44
Modiolus sp.*	239	8.12
Pseudoplacunopsis fissistriata (Winkler)**	11	0.37
Pleuromya cf. *mactroides* (Schlotheim)**	205	6.96
byssate pteriid **	5	0.17
Parallelodon sp.*	6	0.20
Daonella?*	1	<1
Arcid indet.*	1	<1
Pecten indet.*	2	<1
Anodontophora munsteri (Wissman)	1	<1
Total bivalves	543	18.46
Epifaunal bivalves	293	53.96
Infaunal bivalves	250	46.04

Note: * = epifaunal; ** = infaunal.

main poorly documented compared to the famous soft-bodied occurrences such as the Burgess Shale and Mazon Creek faunas that are widely cited in modern studies (Nitecki, 1979; Baird et al., 1985; Whittington and Conway Morris, 1985; Gould, 1989; Butterfield, 1990; Allison and Briggs, 1991; Collins, 1996).

Coenothyris accounts for 100% of the brachiopods in the community, whereas 10 bivalve genera constitute the remaining fauna (table 1). The exposures of Anisian–Ladinian rocks in the Negev and Sinai are discontinuous, making it difficult to collect and study in situ shells laterally for any great distance. Brett et al. (1986) noted this difficulty in locating and tracing simple smothered layers from one outcrop to the next in the Middle Devonian Hamilton Group of New York, although it was possible in many cases. Brett (personal commun.) noted that it may be possible to trace certain smothered layers for considerable distances. Because these layers may preserve original patchy distributions, it may be difficult to find them in given localities, but with careful scrutiny of large areas it is often possible. This suggests that mud

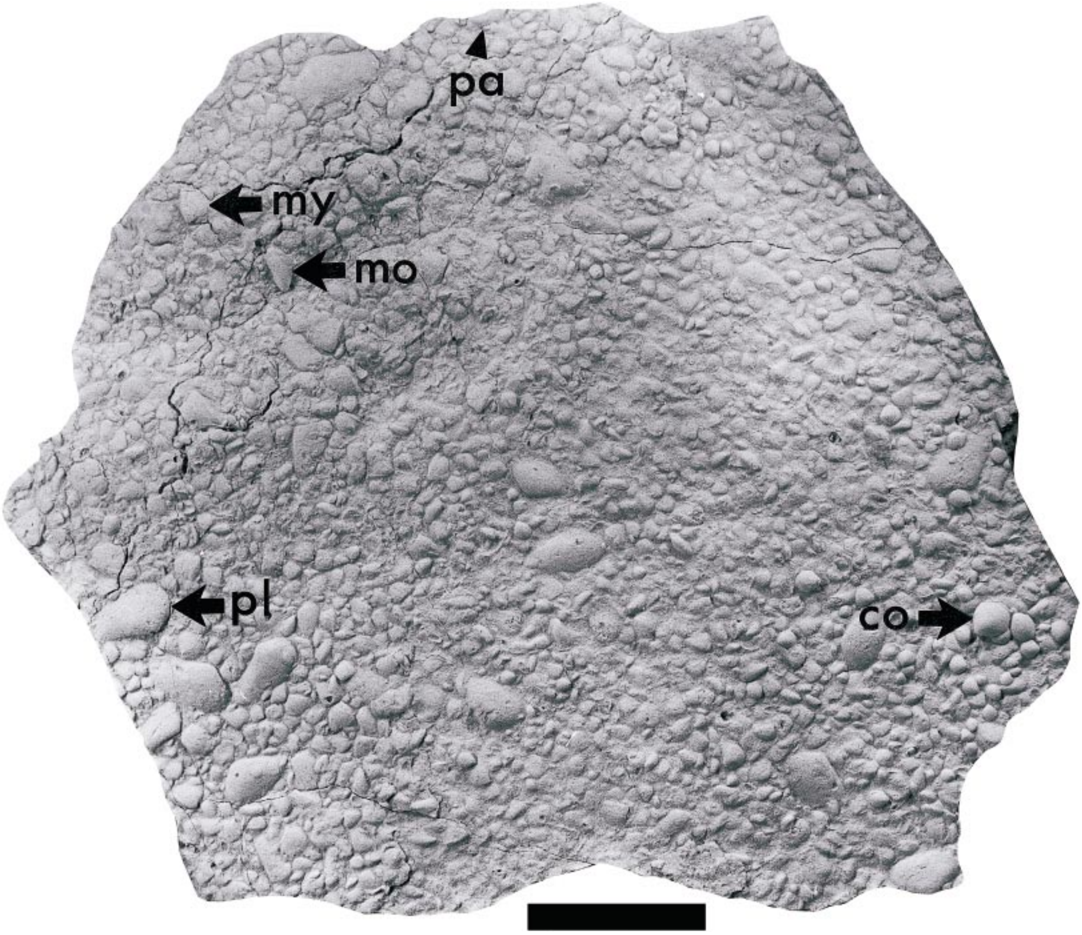

Fig. 3. Slab showing bivalve pavement colonized by *Coenothyris oweni* Feldman, subunit 31, AMNH 46517. Abbreviations: co, *Coenothyris*; pl, *Pleuromya*; mo, *Modiolus*; my, *Myophoria*; pa, *Parallelodon*. Note that this slab has relatively few brachiopods (compare with fig. 4). Scale bar = 4 cm.

obrution sometimes forms a regional sediment blanket rather than being localized fallout from a point input source. Normal populations of *Coenothyris*, that is, those in which there is a complete gradation in size from juvenile to adult, occur in Gebel Areif en-Naqa, Egypt, but no obrution beds containing solely juveniles have been observed there yet.

OBRUTION BED

The *Coenothyris* Bed in the lower part of subunit 31 of the Saharonim Formation (figs. 3, 4) can best be characterized as an obrution bed; that is, very rapid burial of intact brachiopods that resulted in exceptional preservation. A rapid burial event of this type can record brief moments in time or ''snapshots'' of seafloor communities (sensu Brett, 1995; Taylor and Brett, 1996; Brett et al., 1997) and may form important marker horizons in event stratigraphy (Brett et al., 1997). Ager (1974) noted that the characteristics of tempestites, or storm deposits, are that they show evidence of violent disturbance of preexisting sediments followed by their rapid redeposition, all in a shallow water environment. Here, however, there is no indication that preexisting sediments were disturbed. In any case, Ager's (1974) definition for tempestites may be too restrictive in demanding evidence for violent disturbance of preexisting sedi-

Fig. 4. Slab of juvenile specimens of *Coenothyris* that represents an obrution deposit. Note brachiopods in a horizontal to subhorizontal attitude relative to the sediment–water interface, many in dorsal side up position. Large bivalves under the brachiopods are *Pleuromya*. Subunit 31, AMNH 46518. See text for further discussion.

ments. Mud tempestites may be a more appropriate term for indicating the rapid settlement of sediment in relatively low energy settings after a storm (Brett, personal commun.). The *Coenothyris* obrution bed would seem to fall into this category. In most cases there is no direct evidence the preexisting sediments were disturbed, only evidence of rapid redeposition. It is probable that in most cases redeposition was involved. The only other case might be flood washout of muds following the flooding of rivers, but these would be a form of storm deposit in most instances. The brachiopods here need not have been disturbed if they lie below storm-wave base; they will still get the backwash of storm-suspended sediments. The evidence here does suggest deposition below storm-wave base. Stanley (1994) illustrated terebratulid brachiopods in the Early Mesozoic Shalypayco Formation of northern and central Peru that resemble the *Coenothyris* Bed in richness but differ in that the orientations and packing suggest storm deposition.

The burial of immature *Coenothyris* in the Saharonim Formation best conforms to Johnson's (1960) model 1 in which a life assemblage is buried suddenly with no evidence of postmortem transport or exposure (see also Johnson, 1997: fig. 7.7). This community can best be categorized as having a taphonomic grade of ''A'' based on Brandt's (1989) scheme in which there is <10% fossil breakage, >90% articulation, and <10% corrasion/orientation. Johnson's (1960) model 2 describes a more gradual accumulation and burial of shells winnowed by brief postmortem exposure and transport (see, for example, Stanley's [1994: fig. 17] illustration of a bed of Upper Triassic terebratulids where orientations and packing suggest storm deposition; note the high proportion of disarticulated valves), whereas model 3 describes an assemblage altered by long postmortem exposure and appreciable transportation from the original habitat.

The *Coenothyris* Bed does not seem to be hiatal (condensed) or a lag accumulation, as shells are all well preserved and it is not traceable laterally for any great distance. Brett and Baird (1993) considered that a first line of evidence for hiatal concentrations is stratigraphic and that in passive continental margins and epeiric seas these beds display a remarkable lateral persistence, even across major changes in facies of the adjacent beds, although so too are some obrution beds. However, not only condensed beds may show large lateral persistence. Brett and Baird (personal commun.) have traced out many single event obrution beds in the Ordovician–Silurian and Devonian with considerable precision. Indeed, the fact that this occurrence appears localized may require explanation. They suggested (unpublished manuscript) that two mechanisms of mud redeposition may be indicated: (1) widespread layers may indicate hemipelagic sedimentation from detached sediment plumes, and (2) localized occurrences may reflect point source bottom flows (true mud turbidites or distal tempestites).

There is also no evidence of mixtures of fossils representing two or more usually distinct biofacies as described by Kidwell and Bosence (1991) on the obrution horizon (although there is shell mixing in the subsurface horizon), nor is there any indication of corroded or abraded shell fragments typical of environmentally condensed shells beds and simple composite beds. All of the brachiopods are articulated, although not all are in life position. Further indication that the beds are not lag deposits is the lack of any reworked fossil material derived by significant erosional truncation of older strata (Kidwell, 1991).

Seilacher (1990) noted that some groups are more susceptible to catastrophic smothering than others by virtue of their general organization and that sudden mud sedimentation can kill and preserve victims simultaneously. He also mentioned that the echinoderms are one such group because their ambulacral system communicates with the ambient sea water and becomes easily clogged by fine sediment. Although some brachiopods have good sediment shedding mechanisms, they may constitute another such group since they are extremely sensitive to suspended sediment clogging the lophophore. Also, they are sessile and therefore unable to escape burial as can trilobites and crinoids. Datillo (2004) reported on trace fossil evidence that the plectambonitoid brachiopod *Sowerbyella rugosa* from the Ordovician of Kentucky was able to move upward through the sediment to reach the sediment–water interface by snapping its valves. He further noted that if plectambonitoids were able to snap their valves to move through the sediments, strophomenoids might have been able to accomplish the same maneuver. Here, however, the biconvex *Coenothyris* shells differ morphologically from the concavo–convex-geniculated *Sowerbyella rugosa* and were unlikely to have been able to either shed or move through the sediment. If the *Coenothyris* brachiopods were nonpedunculate and able to have assumed a near-vertical, semiinfaunal position to escape catastrophic burial as were the Ordovician *Sowerbyella* shells, they might have escaped burial by ‘‘valve snapping’’.

Coenothyris shells preserved are in perfect condition, with >99.9% of the shells articulated and only three free valves evident (out of 2399 shells studied in the obrution bed). The shells lay directly on the buried surface, in this case a bivalve pavement, and were buried suddenly. Johnson (1989) described an exterminated *Pentamerus* population from the Silurian of Norway that was terminated not solely by the physical disruption of the sea by storm waves, but also by passive suffocation by fine clastic sediments falling out of suspension. Johnson's populations tended to have a high percentage of whole individuals, as is the case with the *Coenothyris* Bed described herein. He concluded that the termination of an immature population was due to an exceptionally severe storm.

OBRUTION EVENT IN RELATION TO DEPOSITIONAL SEQUENCE

The obrution deposit represented by the accumulation and preservation of *Coenothyris* occurs in the lower part of the Fossiliferous Limestone Member, Saharonim Formation. Brett and Seilacher (1991) noted that obrution deposits are most frequently recognized in the late transgressive to early highstand deposits of many successions. According to Druckman (1974b), the Fossiliferous Limestone Member was deposited as part of the transgression that prevailed in the area during Upper Anisian to Lower-Middle Ladinian times. Brett and Seilacher (1991) noted that this empirical relationship is somewhat paradoxical because transgressive sections are relatively the most sediment starved and consequently should contain the least number of burial events. They noted that many condensed sections, however, may accumulate as a stack of very infrequent large depositional events and that major storms may carry siliciclastic or allodapic carbonate sediments into basins that are otherwise almost completely sediment starved. Reworking is not a factor in the preservation of organisms trapped in these deposits because of the deep position of the sea floor.

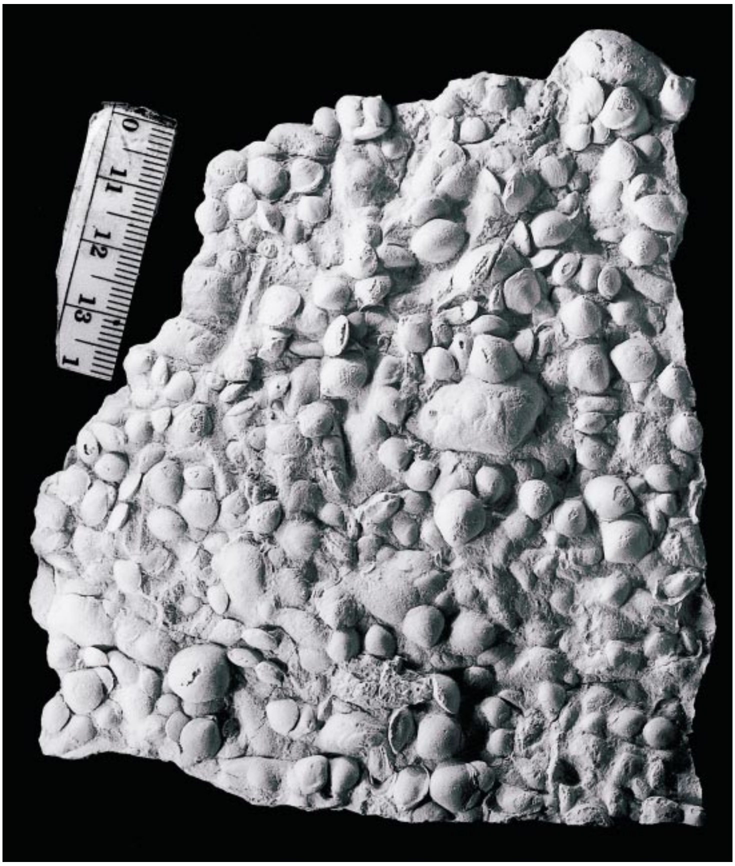

Fig. 5. Slab of juvenile specimens of *Coenothyris*. Note the large *Pleuromya*, just off-center, under which lie disarticulated *Myphoria*. Some shells are slightly exfoliated, but most are almost perfectly preserved. Subunit 31, AMNH 46524. See text for further discussion.

The *Coenothyris* Bed under discussion here is an example of a sediment-starved shell bed that was smothered.

ALLOCHTHONOUS VERSUS AUTOCHTHONOUS BURIAL

Based on examination of the brachiopod and bivalve fauna preserved in the *Coenothyris* Bed, there is no evidence of preferential alignment of valves or hydrodynamic sorting (see figs. 3–5), two criteria noted by Brett and Baird (1993) for recognizing, at least locally, some degree of current reorientation. The elongated shape of the epifaunal *Modiolus* would make that bivalve shell a sensitive indicator of any current that would most likely result in at least a weak alignment of shells. The infaunal bivalves (*Pleuromya*, *Myophoria*) are preserved articulated, but with few specimens in burrows. However, in two cases, both observed in the field, these infaunal bivalves were buried within their burrows, thus ruling out postmortem transport (Brett and Baird, 1993; Kranz, 1974). Most *Coenothyris* shells (89.9%) are preserved in life orientations. Moreover, Alexander (1986) provided evidence that the decay of brachiopod pedicles after death would result in postmortem instability unless they were buried very rapidly. Thus, the obrution bed represents an autochthonous deposit, that is, a deposit of taxa buried in their habitat.

ENVIRONMENT OF DEPOSITION

Druckman (1974b) noted that the occurrence of a diverse benthic and nektic macrofauna, along with the absence of evaporites and dolomites, suggests that deposition of the Saharonim Formation occurred in an open-shelf environment of normal salinity. He further suggested that the complete absence of scouring within the carbonates or signs of channeling and ripple marks implies that most of the member was deposited at least beneath wave base (at a paleolatitude of within 10°N) and may have been deposited even at a depth of between 100 and 200 m. Westermann (1996) suggested that the cephalopod *Monophyllites* (common in the lower part of the Saharonim Formation although not recovered from the *Coenothyris* Bed) indicates a deep ocean environment. However, the marine Middle Triassic series of Israel belongs to the Sephardic Province that sharply differs in its cephalopod composition from coeval ‘‘normal’’ or Panthalassan faunas. Extreme abundance and diversity of nautiloids as in the Triassic of Israel are diagnostic of shallow marine environments according to Bucher (personal commun.). Bucher further noted that the Sephardic Province is also known from Spain and shows some affinities in its abnormal faunal composition and shallow depositional environments with the Germanic Muschelkalk (fig. 6A–C). Triassic phylloceratids such as *Monophyllites* are not, according to Bucher, indicative of deep water, but are generally ubiquitous in ammonoid-bearing beds. In Israel, cephalopods are common only in the deeper more transgressive basins where there is an opening to the Tethys.

Simple layered bottom horizons may be sequentially arranged along a proximal-distal axis, and simple layers, of which the *Coenothyris* Bed is typical, are more common in proximal upslope settings (Brett et al., 1986). However, concretionary and pyritic beds are typical of more distal downslope environments. The depth of the *Coenothyris* Bed may to be similar to that inferred for Johnson’s (1989) *Pentamerus* beds from Norway. He noted that suffocated populations tend to have a high percentage of whole individuals and that whether by fallout below or active disruption above wave base, only the most severe storms appear to have affected these deeper, more offshore sea-floor zones.

The burial increment (sensu Kidwell, 1991) consists of unfossiliferous sediment ranging in thickness from 1.5 to 2 cm that was rapidly deposited in a period that ranged from a few hours to a few days. There is no evidence of fining-upward size gradation or planar and cross lamination that are indicative of deposition from a waning current (Brett, 1990). Brett noted that the burial layer most commonly consists of barren structureless mudstone or siltstone. Here it consists of marl in the lower part and pure clay in the upper part with no evidence of gradation between the two layers. The most likely reason for rapid burial here was that the muds were probably flocculated, causing the suspended particles to behave hydrodynamically as silts or fine sands rather than as muds, as discussed by Brett (1990) and Brett and Taylor (1997). This seems most plausible given the high clay content of the sediment (22% clay in the lower part of the bed, with the remainder consisting of carbonate, no pyrite in the clay fraction, no quartz, mica, or silt, and no indication of volcanics; 100% clay in the upper part, no carbonate, no fine sand or silt). In fact, clay matrix can be seen filling the spaces between the immature brachiopod shells (fig. 7A) in the upper part of the bed, but it is not clearly visible on the sectioned slabs (fig. 7B, C) due to the crumbly nature of the claystone; it spalled off during sectioning. As noted by Brett (1990), most of the best obrution *Lagerstätten* are preserved in and beneath layers of fine-grained sediments, for which extremely rapid sedimentation might seem an impossibility.

A small percentage (10.1%) of the shells (of 2336 counted on bedding surfaces) are inverted, dorsal side up (see appendix), signifying some kind of physical perturbation of the environment during or prior to burial. Taylor and Brett (1996) indicated that environmental disturbances associated with the onset of a storm may have produced changes in salinity, oxygenation, and turbidity that adversely affected the benthos. However, most *Coenothyris* are in a horizontal to subhorizontal attitude relative to the sediment–water interface, ventral side up, indicating clogging of the mantle and subsequent collapse and decay of the pedicle before final burial. Webby and Percival (1983) reported rapid decay after displacement of the soft

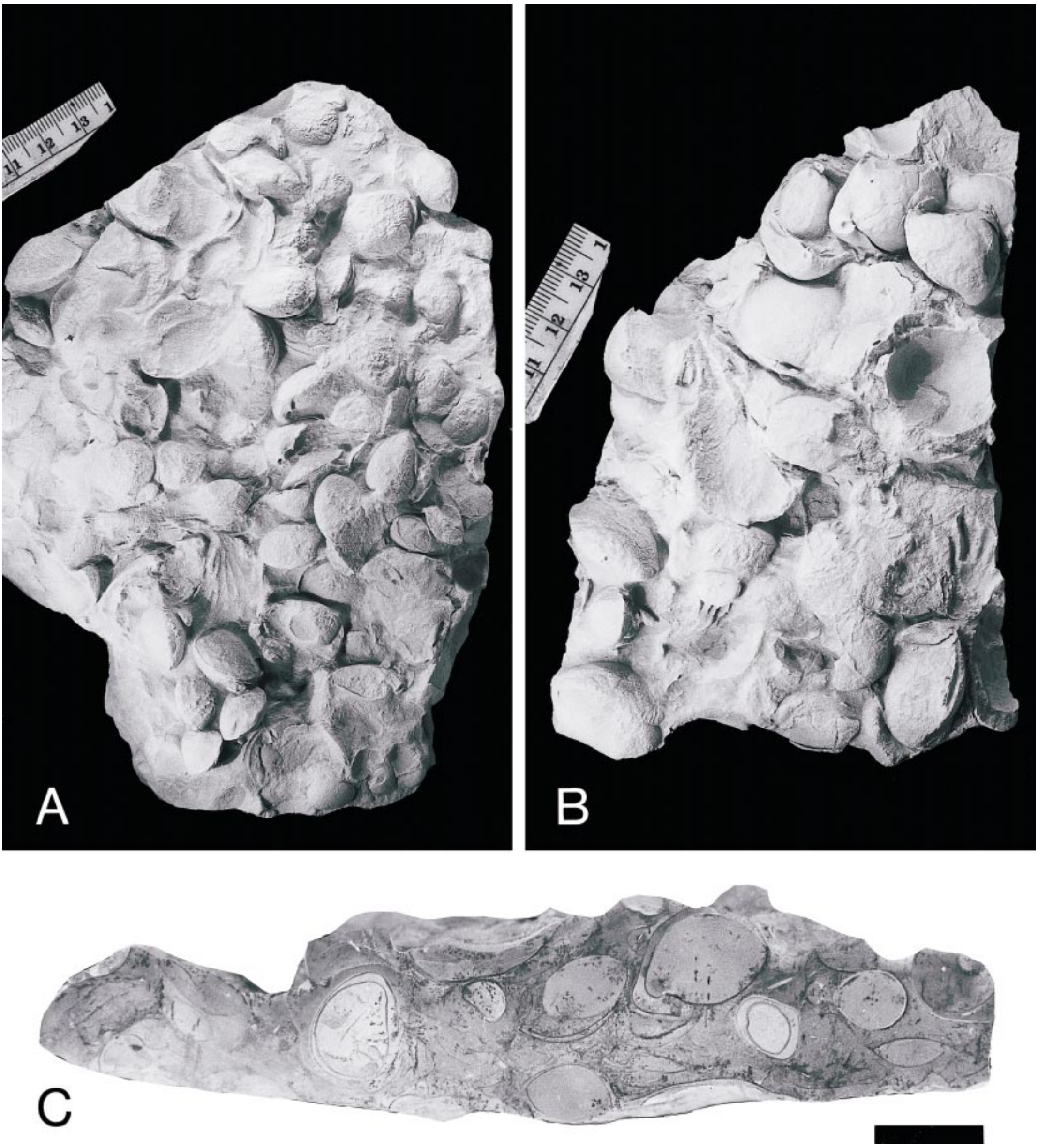

Fig. 6. **A, B.** Slabs with normal populations of *Coenothyris* that range from ephebic to gerontic shells. **A,** Subunit 42, AMNH 46522; **B,** Subunit 42, NHM 1008. **C.** Cross section of *Coenothyris* horizon consisting of jumbled adult specimens similar in appearance to the Triassic German Muschelkalk. Subunit 42, AMNH 46522. Scale bar = 2 cm.

parts of *Eodinobolus*, an inarticulate with no functional pedicle present during ontogeny (Norford and Steele, 1969), from the Ordovician of New South Wales. Here, however, decay of the pedicle occurred before displacement; otherwise, the pedicles would have kept the brachiopod shells attached in a vertical (= living) position. As noted by Boardman et al. (1987), the presence of a pedicle foramen in fossil brachiopods does not necessarily mean that the shell was attached to the substrate by the pedicle. They

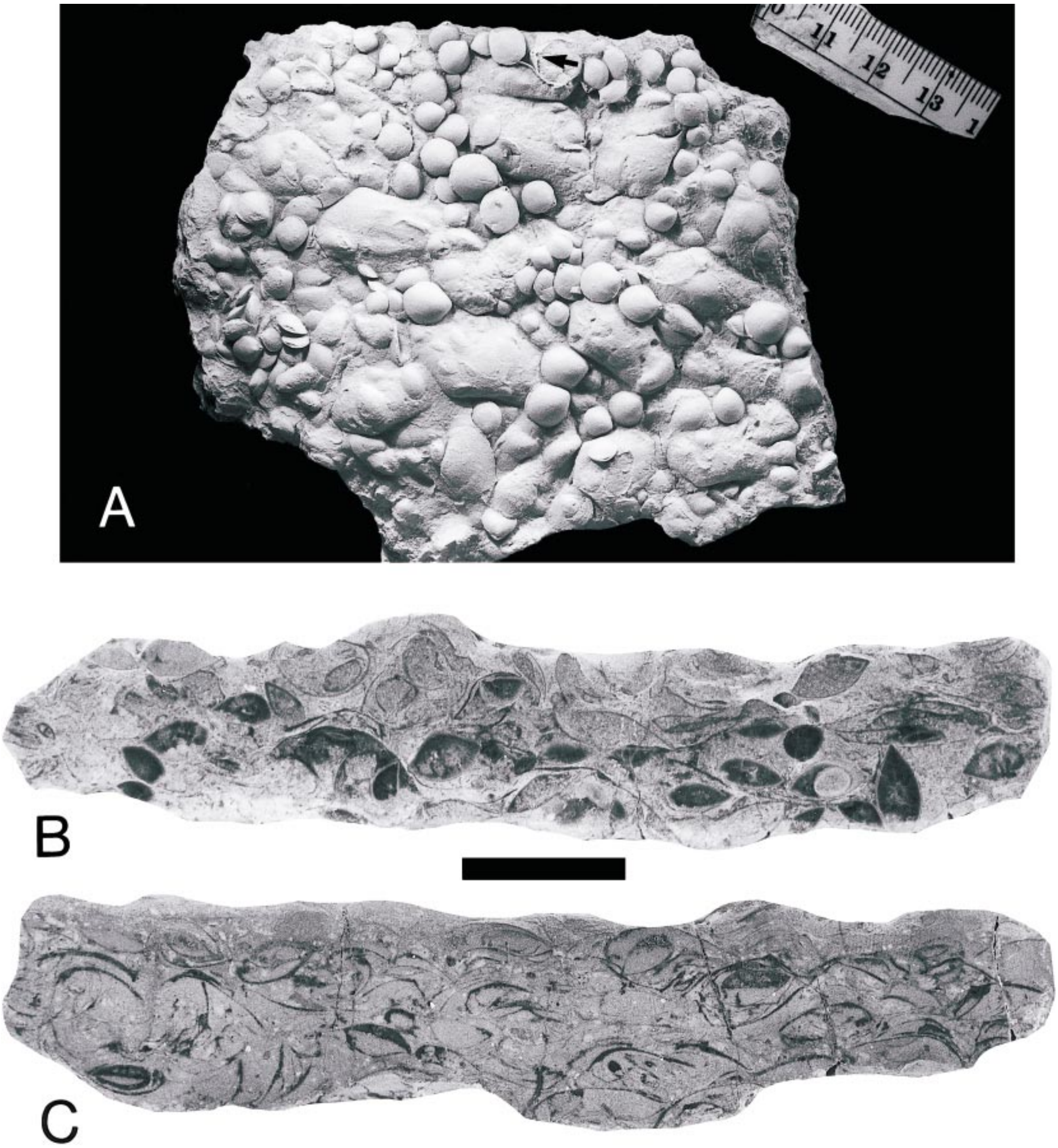

Fig. 7. **A.** Slab of juvenile specimens of *Coenothyris*. Note rare disarticulated ventral valve with small hinge teeth (arrow). Subunit 31, AMNH 46519. **B.** Cross section of *Coenothyris* Bed showing spar-filled articulated shells (bottom half) indicative of rapid burial that did not allow for the decay of soft tissues with subsequent displacement by sediment. The brachiopods just above the spar-filled zone (upper half) are mud filled, indicative of individuals that had died earlier and decayed to become infilled with sediment; approximately 25% of the shells were spar filled. Subunit 31, AMNH 46520. **C.** Cross section of *Coenothyris* Bed showing bivalve hash (composed mainly of the bivalve *Myophoria*) that served as a pavement for brachiopod spat. Subunit 31, AMNH 46521. Scale bar = 2 cm.

further stated that there are some individuals of living species that are attached by their pedicles when hard substrates are available, but are able to adapt a free-lying mode of life when only mud bottoms are present. Here, however, attachment was on a hard bivalve substrate.

In this case *Coenothyris* was smothered by a sudden pulse, or pulses, of clay sedimentation, as a sedimentary event deposit, and subsequently subjected to weak currents. This explains the small percentage of articulated shells dorsal side up. Druckman (1974b) proposed that cyclic alternation of fossiliferous limestone and shale layers on a meter scale in the Lower Saharonim Formation may be due to pulses of terrigenous clay that were supplied to the area over a steady ‘‘background’’ of carbonate precipitation or secretion. However, it seems possible that: (1) there was a change in salinity, and/or (2) there was a change in oxygen levels, and (3) there was an episode of sedimentation that clogged the mantles of the brachiopods resulting in death by anoxia. This was followed by a period of weak current activity that flipped about 10% of the dead shells whose pedicle foramens were either weakened or decayed.

Some shells were buried rapidly, as evidenced by the layer of spar-filled brachiopods (see the lower half of fig. 7B) since rapid entombment does not allow for the decay of soft tissues with subsequent displacement by sediment. Also, the decay of organic matter may increase alkalinity and favor early mineralization. The brachiopods just above the spar-filled zone (fig. 7B, upper half) are mud filled, indicative of individuals that had died earlier and decayed to become infilled with sediment; approximately 25% of the shells were spar filled. There are also some shells with geopetal structure (fig. 7B) that indicates the original orientation of the rock, with the spar-filled upper half representing the ‘‘up’’ position and the spar–mud boundary roughly parallel to the sediment–water interface.

Bioturbation by the burrowing bivalves, mainly by the relatively large *Pleuromya* and the medium-sized *Myophoria*, likely overturned the brachiopods after death. Well-preserved bivalves that formed the burial pavement were probably smothered by a previous influx of sediment too thick to allow them to escape. However, some of the infaunal forms (e.g., *Pleuromya*, *Myophoria*) may have been able to escape death and bioturbate the sediment after the settling of the *Coenothyris* spat. There is no other evidence of disturbance among *Coenothyris*, even minimal disturbance, similar to what Taylor and Brett (1996) reported for their low-level benthic forms (e.g., brachiopods) that were toppled and inverted with minor disarticulation prior to burial. There are no signs of current activity, no ripple marks, no scours of any kind, and no significant numbers of disarticulated shells (3 out of 3000); there is no indication of current activity strong enough to turn the shells upside down. Less than 1% of the bivalves that occur with *Coenothyris* are open, facing down into the sediment—an indication of death position. *Myophoria* valves can be observed (fig. 7B, C) in a concave-down position as a disarticulated hash, but this represents the pavement upon which the *Coenothyris* spat settled and lies directly under the obrution bed. The bed as a whole is time-averaged (see fig. 7C) and includes pavements of bivalve shells that were reworked and stacked. This process facilitated colonization by pedunculate brachiopods in providing a hard substrate for attachment. The shell bed may represent an interval of sediment starvation.

COMMUNITY AND POPULATION STRUCTURE

The *Coenothyris* population is composed of juvenile brachiopods that were rapidly buried after they settled on a shell pavement that consisted of 10 bivalve genera. Whereas there is clearly evidence of time-averaging, which is an assemblage in which the individuals preserved together were not alive at the same time (Flessa, 2003), the community under study here is represented by both the brachiopods and the bivalves (which were likely buried earlier than the brachiopods) found in the lowermost beds of subunit 31. The *Coenothyris* Bed is considered a local paleocommunity since the shelly parts of the original community were collected from a single bed at one outcrop that belong to within-habitat, time-averaged assemblages (Zuschin and

TABLE 2

Statistical Characterization of the *Coenothyris oweni* Cohort, Saharonim Formation (Upper Anisian–Lower Ladinian), Makhtesh Ramon, Southern Israel

	Length	Width	Thickness
Subunit 42			
OR	5.5–27.6	11.5–22.5	2.5–15.1
SD	3.94	3.67	2.58
Subunit 31, top			
OR	4.7–26.3	4.5–30.0	2.2–19.4
SD	3.55	2.88	3.07
Subunit 31, bottom			
OR	3.7–13.3	1.8–5.8	1.8–6.5
SD	2.01	1.65	1.12
Subunits 12–15			
OR	5.5–25.2	4.5–19.4	2.8–13.6
SD	4.01	3.54	2.74

OR, observed range; SD, standard deviation. All measurements in millimeters. Note that normal populations consisting of a morphocline ranging from neanic to mature forms are represented by the shells found in subunits 42, 31 (top) and 12–15 whereas the juvenile population with its noticeably smaller observed range (length 3.7–13.3; width 1.8–5.8; thickness 1.8–6.5) was recognized only in the lower part of subunit 31.

Stanton, 2002). Some of the infaunal bivalves likely escaped immediate death by burrowing. The brachiopods represent a single cohort (table 2) of juvenile mortality of one spatfall. Some workers (e.g., Cloud, 1948) recognized that environmental factors could have produced a subnormal life-span among brachiopod populations. There is no evidence of stunting; the environment was well oxygenated, salinity was normal, and nutrients were abundant, as evidenced by a diverse fauna above and below the obrution bed (see table 3). The shells were preserved in a type 3 deposit (Brett et al., 1997), which is the most common type of obrution deposit, mud tempestites, which are typically preserved in lower-energy settings.

BIOGEOGRAPHY

The Saharonim Formation is similar to the Germanic Muschelkalk in that it consists primarily of fossiliferous, bioturbated, and stromatolitic limestones, marls, shales, occasional sandstones with plant remains and reptile bones, lithographic limestones with fish remains, and a few gypsum intercalations in the upper part of the formation (Hirsch, 1992). Vertebrate remains found elsewhere in the Gevanim and Saharonim formations, not in the same stratigraphic horizon as the *Coenothyris* Bed, include the shark *Hybodus*, the marine reptiles *Nothosaurus*, *Placodus*, and *Psephosaurus* (table 2). The Sephardic Province (Hirsch, 1972) Muschelkalk facies contains endemic or latitudinally restricted taxa such as: *Pseudofurnishius murcianus*, *Sephardiella mungoensis* (conodonts), *Gevanites epigonus*, *Israelites ramonensis*, *Protrachyceras hispanicum* (ammonites), *Myophoria coxi*, and *Gervillia joleaudi* (bivalves). According to Hirsch (1992), their equivalents in the Germanic Muschelkalk are equally restricted neogondolellid conodonts and various ceratidid ammonite taxa, as well as endemic species of cosmopolitan bivalve genera. There are distinct differences between the Sephardic Province faunas that can be recognized on the southern margin of the Tethys shelf and the Germanic (= Muschelkalk) Province and Tethyan Realm faunas to the north (see Hirsch, 1992: fig. 1; Marquez-Aliaga et al., 1986).

Coenothyris vulgaris shells from the Muschelkalk of France and Germany differ from the Israeli shells in that it they are larger and have a distinctly uniplicate anterior commissure. *Coenothyris vulgaris* from the Upper Muschelkalk (*Terebratula* Bed) of the Holy

TABLE 3

Faunal Constituents of the Fossiliferous Limestone Member, Saharonim Formation (Upper Anisian–Lower Ladinian), Makhtesh Ramon, Southern Israel

Microfossils

- Conodonts
    - *Pseudofurnishius murcianus*
    - *Lonchodina mulleri*
    - *Enanthiognathus ziegleri*
    - *Hibbardella magnidentata*
    - *Hindeodella* sp.
- Ostracodes
    - *Reubenella avnimelechi*
- Foraminifera
    - Indet. miliolids

Megafossils

- Brachiopods
    - *Coenothyris oweni* Feldman
    - *Lingula* sp.
    - *Dielasma julicum* (Bittner)
- Echinoderms
    - *Encrinus* sp.
- Bivalves
    - *Leda* cf. *fibula* Mansuy
    - *Palaeoneilo elliptica* (Goldfuss)
    - *Lyriomyophoria elegans* (Dunker)
    - *Myophoria germanica* (Hohenstein)
    - *Costatoria coxi* (Awad)
    - *C. multicostata* (Lerman)
    - *Neoschizodus laevigatus* (Ziethen)
    - *Myophoriopsis cf. subundata* (Schauroth)
    - *Pseudoplacunopsis fissistriata* (Winkler)
    - *P.* cf. *ostracina* (Schlotheim)
    - *Placunopsis* cf. *flabellum* Schmidt
    - *Ostrea montis-caprilis* Klipstein
    - *Modiola* cf. *raibliana* Bittner
    - *M.* cf. *salzstettensis* Hohenstein
    - *Cassianella* cf. *decussata* (Munster)
    - *Cassianella* spp.
    - *Gervillia joleaudi* Schmidt
    - *G.* aff. *alberti* (Goldfuss)
- Bivalves (continued)
    - *G.* cf. *bouei* (Hauer)
    - *Lima striata* (Schlotheim)
    - *Lima* sp.
    - *Mysidioptera* cf. *vix-costata* (Stoppani)
    - *Pecten discites* (Schlothheim)
    - *P. albertii* (Goldfuss)
    - *Schafhautlia* aff. *mellingi* (Hauer)
    - *Anodontophora munsteri* (Wissmann)
    - *Pleuromya* cf. *mactroides* (Schlotheim)
- Gastropods
    - *Naticopsis* sp.
    - *Zygopleura* spp.
    - *Omphaloptycha* sp.
- Cephalopods
    - *Mojsvaroceras* cf. *morloti* (Mojsisovics)
    - *M.* cf. *augusti* (Mojsisovics)
    - *Germanonautilus salinarius* (Mojsisovics)
    - *G. bidorsatus* (Schlotheim)
    - *G.* cf. *advena* (Fritsch)
    - *Indonautilus awadi* Kummel
    - "*Ceratites*" spp.
    - *Israelites ramonensis* Parnes
    - *Negebites zaki* Parnes
    - *Protrachyceras wahrmani* Parnes
    - *P. curionii* Mojsisovics
    - *P.* cf. *ladinum* Mojsisovics
    - *P.* cf. *hispanicum* Mojsisovics
    - *P.* cf. *mascagnii* Tornquist
    - *Proarcestes* sp.
    - *Monophyllites* cf. *sphaerophyllus* (Hauer)
- Vertebrates
    - *Hybodus* sp.
    - *Nothosaurus* spp.
    - *Palcodus* sp.
    - *Psephosaurus picardi* Brotzen
    - *Psephosaurus* sp.

Cross Mountains, central Poland, and specimens from Bukowie, at the northeastern border of the Holy Cross Mountains, also display a distinct sulcation of the anterior commissure. *Coenothyris acuta* from Stara Planina Mountain in the Yugoslavian Carpartho-Balkanides has a strongly biplicate anterior commissure, folded shell surface, and carinate beak, whereas *C. radulovici* from the same locality differs in its elongate oval outline and varying uniplicate to rectimarginate anterior commissure. The anterior commissure of *C. oweni* is invariably rectimarginate. There is a distinct morphologic similarity between the Israeli shells and those from the European Muschelkalk indicating some proximity, the degree of which, however, is difficult to determine. *Coenothyris oweni* in the Triassic beds of southern Israel allows for an enhanced correlation with Muschelkalk strata in Europe and enables Tethyan Realm faunas to be more easily distinguished from faunal elements of the Sephardic Province.

CONCLUSIONS

A *Coenothyris* brachiopod community recovered from the Middle Triassic (Upper Anisian–Lower Ladinian) of southern Israel is unique in that it (1) is comprised solely of juveniles, and (2) represents an obrution deposit. *Coenothyris oweni* Feldman accounts for 100% of the brachiopods in the community, whereas 10 bivalve genera constitute the remaining fauna. The horizon is not a condensed bed or lag accumulation since it is not traceable laterally for any great distance, and there is no evidence of any reworked fossil material derived by significant erosional truncation of older strata. Brachiopods may constitute a group that is more susceptible to catastrophic smothering than others since they are extremely sensitive to suspended sediment that can clog the mantle. The depositional environment was that of a normal, calm, relatively shallow marine sea on an open shelf. An absence of scouring, channelling, or ripple marks implies deposition at least beneath wave base.

Juvenile *Coenothyris* were buried rapidly by pulses of clay sedimentation probably in the form of flocculated muds, causing suspended particles to act as silts or fine sands rather than as muds. Most of the shells are in a horizontal to subhorizontal attitude relative to the sediment–water interface, ventral side up, indicating mantle clogging and subsequent collapse and decay of the pedicle before final burial. Some brachiopods (about 10%) were overturned after burial by burrowing bivalves such as *Pleuromya* and *Myophoria* that also homogenized the sediment.

The community under study here shows evidence of time-averaging and is represented by both the brachiopods and the bivalves found in the lower part of subunit 31. Here we have a local paleocommunity since the shelly parts of the original community were collected from a single bed at one outcrop that belongs to within-habitat, time-averaged assemblages. The brachiopods represent a single cohort of juvenile mortality of one spatfall. There is no evidence of stunting, and the shells were preserved in a type 3 deposit, which is the most common type of obrution deposit, mud tempestites, which are typically preserved in lower energy settings.

Biogeographically, the *Coenothyris* community belongs to the Sephardic Province, also known from Spain, which is similar in its faunal composition and shallow depositional environments with the Germanic Muschelkalk. The presence of the brachiopod *Coenothyris* in southern Israel is useful in correlating the Triassic rocks in the Negev with those in Europe and helps differentiate the Sephardic Province from the Germanic Muschelkalk and the Tethyan realm faunas to the north.

ACKNOWLEDGMENTS

The work was supported by the National Geographic Society and carried out during my tenure as a visiting scientist at the Geological Survey of Israel, Jerusalem. I am especially grateful to C.E. Brett (University of Cincinnati, Cincinnati, Ohio) for stimulating comments, suggestions for improving the manuscript, and access to unpublished data. I thank the following for discussion and criticism of the text: C. Benjamini (Ben Gurion University, Beersheva, Israel), H. Bucher (Université Claude Bernard, Lyon, France), N. Eldredge (AMNH), F. Hirsch (GSI), N. Landman (AMNH), R.H. Lindemann (Skidmore College, Saratoga Springs, NY), N.D. Newell (AMNH), E.F. Owen (NHM), and M.R. Sandy (University of Dayton). P. Rollings (AMNH) deserves thanks for assisting in photographic work, and S. Klofak (AMNH) helped in the preparation of specimens. Thanks also to two anonymous reviewers for their insightful comments and suggestions.

REFERENCES

Ager, D.V. 1974. Storm deposits in the Jurassic of the Moroccan High Atlas. Palaeogeography, Palaeoclimatology, Palaeoecology 15: 83–93.

Alexander, R.R. 1986. Life orientation and postmortem reorientation of Chesterian brachiopods shells by paleocurrents. Palaios 1: 303–311.

Allison, P.A., and D.E.G. Briggs. 1991. Taphonomy: releasing the data locked in the fossil record. New York: Plenum Press.

Awad, G.H. 1946. On the occurrence of Marine Triassic (Muschelkalk) deposits in Sinai. Bulletin de L'Institut d'Égypte 27: 397–427.

Baird, G.C., S.D. Sroka, S.W. Shabica, and T.L. Beard. 1985. Mazon Creek-type fossil assemblages in the U.S. midcontinent Pennsylvanian: their recurrent character and paleoenvironmental significance. *In* A. Seilacher, W.E. Reif, and F. Westphal (editors), Sedimentological, ecological and temporal patterns of fossil Lagerstätten: 87–98. Philosophical Transactions of the Royal Society of London B311: 87–98.

Bartov, Y., Z. Lewy, G. Steinitz, and I. Zak. 1980. Mesozoic and Tertiary stratigraphy, paleogeography and structural history of the Gebel Areif en-Naqa area, eastern Sinai. Y.K. Bentor Honourary Volume, Israel Journal of Earth Science 29: 114–139.

Bender, F. 1968. Geologie van Jordanien. Berlin Gebrueder Borntraeger, Berlin-Stuttgart, 230 pp.; also 1974, Geology of Jordan, translated by M.K. Khdeir et al., Beitrage zur Regionalen Geologie der Erde, Supplementary [English] Edition 7: 1–196.

Bentor, Y.K., U. Golani, L. Picard, A. Vroman, and I. Zak. 1965. The geological map of Israel, 1: 250,000 (2 sheets). Tel Aviv: Survey of Israel.

Boardman, R.S., A.H. Cheetham, and A.J. Rowell (editors). 1987. Fossil invertebrates. Palo Alto, CA: Blackwell Scientific Publications.

Brandt, D.S. 1989. Taphonomic grades as a classification for fossiliferous assemblages and implications for paleoecology. Palaios 4: 303–309.

Brett, C.E. 1990. Obrution deposits. *In* D.E.G. Briggs and P.R. Crowther (editors), Palaeobiology: a synthesis: 239–243. Oxford: Blackwell Scientific Publications.

Brett, C.E. 1995. Sequence stratigraphy, biostratigraphy, and taphonomy in shallow marine environments. Palaios 10: 597–616.

Brett, C.E., and G.C. Baird. 1993. Taphonomic approaches to temporal resolution in stratigraphy: examples from Paleozoic marine mudrocks. *In* S.M. Kidwell and A.K. Behrensmeyer (editors), Taphonomic approaches to time resolution in fossil assemblages: 250–274. Boston: The Paleontological Society.

Brett, C.E., G.C. Baird, and S.E. Speyer. 1997. Fossil Lagerstätten: stratigraphic record of paleontological and taphonomic events. *In* C.E. Brett and G.C. Baird (editors), Paleontological events: stratigraphic, ecological, and evolutionary implications: 3–40. New York: Columbia University Press.

Brett, C.E., and A. Seilacher. 1991. Fossil Lagerstätten: a taphonomic consequence of event sedimentation. *In* G. Einsele, W. Ricken, and A. Seilacher (editors), Cycles and events in stratigraphy: 283–297. Berlin: Springer-Verlag.

Brett, C.E., S.E. Speyer, and G.C. Baird. 1986. Storm-generated sedimentary units: tempestite proximality and event stratification in the Middle Devonian Hamilton Group of New York. *In* C.E. Brett (editor), Dynamic stratigraphy and depositional environments of the Hamilton Group (Middle Devonian) in New York State, part I. New York State Education Department, Bulletin 457: 129–156.

Brett, C.E., and W.L. Taylor. 1997. The *Homocrinus* beds: Silurian crinoid Lagerstätten of western New York and southern Ontario. *In* C.E. Brett and G.C. Baird (editors), Paleontological events: stratigraphic, ecological, and evolutionary implications: 181–223. New York: Columbia University Press.

Butterfield, N.J. 1990. Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. Paleobiology 16: 272–286.

Cloud, P.E., Jr. 1948. Assemblages of diminutive brachiopods and their paleoecological significance. Journal of Sedimentary Petrology 18: 56–60.

Collins, D. 1996. The ‘‘evolution’’ of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov.) and order Radiodonta (nov.). Journal of Paleontology 70: 280–293.

Cox, L.R. 1924. A Triassic fauna from the Jordan Valley. Annals and Magazine of Natural History 14: 52–96.

Datillo, B.F. 2004. A new angle on strophomenid paleoecology: trace-fossil evidence of an escape response for the plectambonitoid brachiopod *Sowerbyella rugosa* from a tempestite in the Upper Ordovician Kope Formation (Edenian) of northern Kentucky. Palaios 19: 332–348.

Douvillé, H. 1879. Sur quelques genres de brachiopodes Terebratulidae et Waldheimiidae. Société Géologique de France, Bulletin 7: 251–277.

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

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

Druckman, Y. 1974b. Stratigraphy of the Triassic sequence in southern Israel. Geological Survey of Israel Bulletin 64: 1–94.

Druckman, Y. 1976. The Triassic in southern Israel and Sinai: a sedimentological model of marginal, epicontinental, marine environments.

Unpublished Ph.D. dissertation, Hebrew University, Jerusalem, 188 pp. [in Hebrew, English summary]

Duméril, A.M.C. 1806. Zoologique analytique ou méthode naturelle de classification des animaux. Paris: Allais.

Feldman, H.R. 1986. Cladistic analysis of a Jurassic rhynchonellid brachiopod genus from the Middle Eastern Ethiopian Province. Abstracts of the Geological Society of America Northeastern Section Meeting, Kiamesha Lake, New York 18: 16.

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

Feldman, H.R. 2002. A new species of *Coenothyris* (Brachiopoda) from the Triassic (Ladinian) of Israel. Journal of Paleontology 76: 34–42.

Feldman, H.R., and C.E. Brett. 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 brachiopod communities: trophic structure, diversity, substrate relations and niche replacement. Third North American Paleontological Convention Proceedings, Montreal, Canada 1: 169–174.

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., and E.F. Owen. 1993. Vicariance biogeography of the Middle Eastern Ethiopian Province: implications for the Paleozoic. Abstracts of the Geological Society of America Annual Meeting, Boston, Massachusetts 25: 55.

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.

Flessa, K.W. 2003. Time-averaging. *In* D.E.G. Briggs and P.R. Crowther (editors), Palaeobiology 2: 292–296. Oxford: Blackwell Science.

Garfunkel, Z., and B. Derin. 1985. Permian-Early Mesozoic tectonism and continental margin formation in Israel and its implications for the history of the eastern Mediterranean. *In* J.E. Dixon and A.H.F. Robertson (editors), The geological evolution of the eastern Mediterranean: 187–201. Oxford: Blackwell Scientific Publications.

Gould, S.J. 1989. Wonderful life: the Burgess Shale and the nature of history. New York: Norton.

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

Hirsch, F 1992. Circummediterranean Triassic eustatic cycles. Israel Journal of Earth Sciences 40: 29–38.

Hirsch, F., J-P. Bassoullet, É. 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. Crasquin-Soleau and É. Barrier (editors), Peri-Tethys memoir 4: epicratonic basins of Peri-Tethyan platforms. Mémoires du Muséum National d'Histoire Naturelle 179: 213–235.

Huxley, T.H. 1869. An introduction to the classification of animals. London: John Churchill and Sons.

Johnson, M.E. 1989. Tempestites recorded as variable *Pentamerus* layers in the Lower Silurian of southern Norway. Journal of Paleontology 63: 195–205.

Johnson, M.E. 1997. Silurian event horizons related to the evolution and ecology of penatmerid brachiopods. *In* C.E. Brett and G.C. Baird (editors), Paleontological events: stratigraphic, ecological, and evolutionary implications: 162–180. New York: Columbia University Press.

Johnson, R.J. 1960. Models and methods for analysis of the mode of formation of fossil assemblages. Geological Society of America Bulletin 71: 1075–1086.

Kidwell, S.M. 1991. The stratigraphy of shell concentrations. *In* P.A. Allison and D.E.G. Briggs (editors), Taphonomy: releasing the data locked in the fossil record: 211–290. New York: Plenum Press.

Kidwell, S.M., and P. Bosence. 1991. Taphonomy and time averaging of marine shelly faunas. *In* P.A. Allison and D.E.G. Briggs (editors), Taphonomy: releasing the data locked in the fossil record: 116–209. New York: Plenum Press.

Kranz, P.M. 1974. The anastrophic burial of bivalves and its paleoecological significance. Journal of Geology 82: 237–265.

Marquez-Aliaga, A., F. Hirsch, and A.C. Lopez-Garrido. 1986. Middle Triassic bivalves from Hornos-Siles, Sephardic Province. Neues Jahrbuch für Geologie und Palaeontologie, Abhandlungen 173: 201–227.

Mazor, E. 1955. The magmatic occurrences in Makhtesh Ramon. Geological Survey of Israel, 29 pp. [unpublished report, in Hebrew]

Nitecki, M.H. (editor). 1979. Mazon Creek fossils. New York: Academic Press.

Norford, B.S., and H.M. Steele. 1969. The Ordovician trimerellid brachiopod *Eodinobolus* from south-east Ontario. Palaeontology 12: 161–171.

Parnes, A. 1975. Middle Triassic ammonite biostratigraphy in Israel. Geological Survey of Israel Bulletin 66: 1–35.

Parnes, A. 1986. Middle Triassic cephalopods from the Negev (Israel) and Sinai (Egypt). Geological Survey of Israel Bulletin 79: 1–59.

Picard, L. 1951. Geomorphogeny of Israel, Part I: The Negev. Bulletin of the Research Council of Israel Bulletin, Section G, Geo-sciences G1: 5–32.

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

Popiel-Barczyk, E., and H. Senkowiczowa. 1989. Representatives of the genus *Coenothyris* Douvillé, 1879, from the Terebratula Bed (Upper Muschelkalk) of the Holy Cross Mountains, central Poland. Acta Geologica Polonica 39: 93–112.

Schuchert, C. 1913. Class 2. Brachiopoda. *In* K.A. von Zittel (translated and edited by C.R. Eastman), Text-book of palaeontology vol. 1, 2nd ed.: 355–420. London: Macmillan.

Seilacher, A. 1990. Taphonomy of fossil-lagerstätten: overview. *In* D.E.G. Briggs and P.R. Crowther (editors), Palaeobiology: a synthesis: 266–270. Oxford: Blackwell Scientific Publications.

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

Stanley, G.D., Jr. 1994. Early Mesozoic carbonate rocks of the Pucara Group in northern and central Peru. Palaeontographica 233: 1–32.

Taylor, W.L., and C.E. Brett. 1996. Taphonomy and paleoecology of echinoderm *Lagerstätten* from the Silurian (Wenlockian) Rochester Shale. Palaios 11: 118–140.

Waagen, W.H. 1883. Salt Range fossils, part 4(2) Brachiopoda. Memoirs of the Geological Survey of India, Palaeontologica Indica, series 13, 1 fascicule 2: 391–546.

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.

Weisbrod, T. 1976. The Permian in the Near East. *In* H. Falke (editor), the Continental Permian in central, west and south Europe. NATO Advanced Study Institute Series 22: 200–214. Dordrecht, Holland: D. Reidel Publishing Group.

Webby, B.D., and I.G. Percival. 1983. Ordovician trimerellacean brachiopod shell beds. Lethaia 16: 215–232.

Westermann, G.E.G. 1996. Ammonoid life and habitat. *In* N.H. Landman, K. Tanabe, and R.A. Davis (editors), Ammonoid paleobiology: 608–707. New York: Plenum Press.

Whittington, H.B., and S. Conway Morris. 1985. Extraordinary fossil biotas: their ecological and evolutionary significance: Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences 311: 1–192.

Zak, I. 1957. The Triassic in Makhtesh Ramon. Unpublished M.A. thesis, Hebrew University, Jerusalem, 84 pp. [in Hebrew, English summary]

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

Zak, I. 1964. The Triassic in Areif en-Naqa, Sinai. Israel Geological Survey Report Geochemistry Department no. 64/1, 28 pp., appendices. [in Hebrew, English summary]

Zuschin M., and R.J. Stanton, Jr. 2002. Paleocommunity reconstruction from shell beds: a case study from the Main Glauconite Bed, Eocene, Texas. Palaios 17: 602–614.

APPENDIX

NUMBERED SLABS COLLECTED FROM OBRUTION BED (SUBUNIT 31, LOWER PART) OF FOSSILIFEROUS LIMESTONE MEMBER (UPPER ANISIAN-LOWER LADINIAN), SAHARONIM FORMATION (ANISIAN-CARNIAN) AT HAR GEVANIM, MAKHTESH RAMON, SOUTHERN ISRAEL

This list denotes the number of *Coenothyris oweni* found dorsal valve up (= overturned) and the number and percentage (in parentheses) found ventral valve up (in a horizontal to subhorizontal attitude relative to the sediment-water interface and consequently an inferred life position; see text for further discussion).

AMNH number	Dorsal valve up	Ventral valve up
46517, slab #1	21	144 (87.3%)
46518, slab #2	20	175 (89.7%)
46519, slab #3 [One free ventral valve]	22	81 (78.6%)
46520, slab #4	4	61 (93.8%)
46521, slab #5 (no preserved brachiopods)		
46523, slab #6	10	260 (96.3%)
46524, slab #7	10	192 (95.0%)
46525, slab #8 [One free dorsal valve]	11	93 (89.4%)
46526, slab #9	6	44 (88.0%)
46527, slab #10	24	139 (85.3%)
46528, slab #11	22	225 (91.0%)
46529, slab #12	1	13 (92.9%)
46530, slab #13	33	189 (85.1%)
46531, slab #14	17	208 (92.4%)
46532, slab #15	1	9 (90.0%)
46533, slab #16	2	14 (87.5%)
46534, slab #17	0	5 (100%)
46535, slab #18 (no preserved brachiopods)		
46536, slab #19	3	51 (94.4%)
46537, slab #20	5	22 (81.5%)
46538, slab #21 (no preserved brachiopods)		
46539, slab #22 (no preserved brachiopods)		
46540, slab #23	20	120 (87.5%)
46541, slab #24	4	52 (92.9%)
46542, slab #25	0	3 (100%)
Totals	236	2100 (89.9%)

Complete lists of all issues of the *Novitates* and the *Bulletin* are available at World Wide Web site http://library.amnh.org/pubs. Inquire about ordering printed copies via e-mail from scipubs@amnh.org or via standard mail from: American Museum of Natural History, Library—Scientific Publications, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009.

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).