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TUNETHYRIS BLODGETTI SP. NOV. (BRACHIOPODA, TEREBRATULIDA) FROM THE MIDDLE TRIASSIC OF MAKHTESH RAMON, SOUTHERN ISRAEL

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Abstract: *Tunethyris blodgetti* sp. nov. from the Triassic Saharonim Formation, Makhtesh Ramon, an erosional cirque in southern Israel, is erected on the basis of a suite of 39 articulated specimens. The shells are very strongly sulciplicated, a feature that seems to be more prevalent in the Mesozoic than the Palaeozoic. The Saharonim Formation was deposited under quasi-normal, calm, relatively shallow marine conditions. Faunal constituents of the Saharonim Formation include conodonts, ostracods, 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 may help differentiate the Sephardic Province from the Germanic Muschelkalk and the Alpine Tethyan faunas to the north.

Key words: Brachiopoda, Triassic, Sephardic Province, Ladinian, Makhtesh Ramon, palaeoecology, palaeobiogeography.

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INTRODUCTION

The first recognition of Triassic rocks in the Middle East was the discovery of Carnian fossils near Latakia in Syria, in 1915 (Picard and Flexer, 1974). A Triassic fauna was collected in Transjordan by the Turkish Petroleum Company (Cox, 1924). Awad (1946) noted the occurrence of 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 during World War II in what is now southern Israel. 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). Triassic rocks that crop out in southern Israel (Makhtesh Ramon) were described by Druckman (1969, 1974a, b, 1976) and Zak (1957).

The lower part of the Fossiliferous Limestone Member of the Saharonim Formation, from which the new species was collected, contains the *Paraceratitoides brotzeni* Horizon, belonging to the uppermost Anisian. The upper part of the member contains the *Protrachyceras curionii* var. *ramonenesis* Horizon, considered to be lowermost Ladinian. Near the top, the conodont *Pseudofurnishius murcianus*, which occurs no earlier than the early Ladinian, was recovered. This subunit is extremely rich in marine fossils (e.g., *Leda* cf. *fibula*, *Palaeoneilo elliptica*, *Elegantia elegans*, *Lyriomyphoria germanica*, *Costatoria coxi*, *Costatoria multicostata*, *Neoschizodus laevigatus*, *Myophoriopis* cf. *subundata*, *Pseudoplacunopsis fissistriata, Pseudoplacunopsis* cf. *ostracina*, *Placunopsis* cf. *flabellum*, *Ostrea montiscaprilis*, *Modiola* cf. *raibliana*, *Modiola* cf. *salzstettensis*, *Cassianella* cf. *decussata*, *Cassianella* sp., *Gervillia joleaudi*, *Gervillia* aff. *alberti*, *Gervillia* cf. *bouei*, *Lima striata*, *Lima* sp., *Mysidioptera* cf. *vixcostata*, *Entolium discites*, *Pecten albertii, Schafhautlia* aff. *mellingi*, *Anodontophora munsteri*, *Pleuromya* cf. *mactroides*, *Naticopsis* sp., *Zygopleura* sp., and *Omphaloptycha* sp.; see Lerman, 1960; Parnes, 1962). Crinoids, brachiopods, ammonoids, nautiloids, ophiuroids, vertebrates (mostly reptiles), ostracods, and conodonts are also abundant. This fauna contains many endemic ammonoids, belonging to *Paraceratites*, *Israelites*, *Negebites*, *Gevanites*, and *Protrachyceras* (Parnes, 1962, 1975, 1986). These are defining forms of the Sephardic Realm, the faunal realm that extended across the south Neotethyan shelf from the Near East to the western Mediterranean. The Limestone and Marl Member, at the base of 9 m of dark, nodular, bioturbated micrites, is reminiscent of the ‘calcaires vermiculés’ in Europe. This facies is overlain by fossiliferous limestones and marls with oolites, stromatolites, small molluscan mounds, flat pebble conglomerates, and

Fig. 1. Satellite image of the eastern Mediterranean and adjacent countries (taken from https://www.google.com/permissions/ geoguidelines/attr-guide.html). The collection locality at Har Gevanim, Makhtesh Ramon, southern Israel, is denoted by the arrow. Israel grid coordinates 1370/9998-1379/9994; GPS N 30.58587497°, E 34.87624599°.

several evaporite/dolomite/shale horizons, indicating marine environments, ranging from offshore to intertidal. A brief offshore episode in indicated by the *Gevanites epigonus* Horizon of the Late Lower Ladinian with additional ammonoids *Gevanites epigonus* and *Gevanites cornutus*. The conodont *Pseudofurnishius murcianus* also occurs here.

Ammonoid nomenclature in this paper is after Parnes *et al*. (1985).

GEOLOGICAL SETTING

The specimens described in this paper were collected at Har Gevanim in Makhtesh Ramon, a large (40 km long, 8 km wide), northeast-trending erosional cirque, part of the Ramon Anticline, in southern Israel (Fig. 1). In addition to the Triassic sediments exposed in the study area, there are Jurassic–Cretaceous beds that cover large parts of the interior of the erosional cirque, as well as alkaline trachybasaltic to trachysyenitic dikes and sills and larger intrusive bodies, such as an essexitic laccolith and nordmarkite boss (Picard and Flexer, 1974). The material was collected from the lower members of the Triassic (Anisian–Ladinian) Saharonim Formation (Fig. 2). The lowermost Fossiliferous Limestone Member consists of limestone beds alternating with shales. Many of the limestones are fossiliferous and some of the shale is calcareous. The overlying Limestone and Marl Member consists of bioturbated micrites, overlain by fossiliferous limestones and marls.

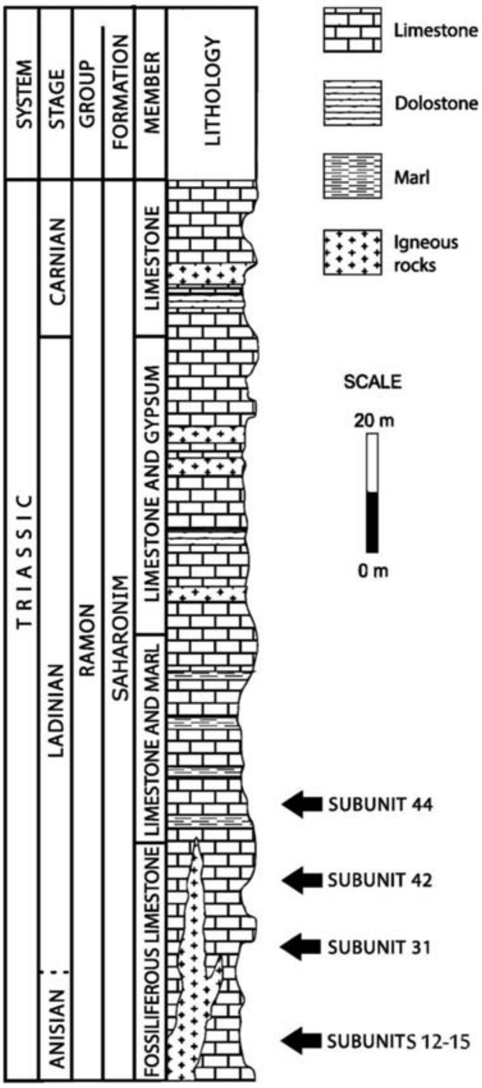

Fig. 2. Generalized columnar section of the Triassic Saharonim Formation at Har Gevanim, Makhtesh Ramon, southern Israel. For detailed stratigraphy see Druckman (1974b) and Parnes (1986). Arrows represent occurrences of *Tunethyris* and *Coenothyris* beds at marked subunit intervals. Subunit designations are after Zak (1964) and Parnes (1975).

The ammonite *Gevanites epigonus*, indicative of the upper Fassanian (lower Ladinian *Euprotrachyceras gred-*

leri Zone), is found in the Limestone and Marl Unit of the Saharonim Formation.

This study is a continuation of an ongoing project on the taxonomy, biogeography and palaeoecology of Triassic and Jurassic faunas, emphasizing the brachiopods, in the Middle East (Feldman *et al*., 1982, 1991, 2012, 2013, 2014; Feldman, 1986, 1987, 2013; Feldman and Owen, 1988, 1993; Feldman and Brett, 1998; Hirsch *et al*., 1998). Endemic faunas of the Jurassic Ethiopian province 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.

MATERIALS AND METHODS

All shells in the collection are articulated. Transverse serial sections were prepared with a WOKO 50P grinding machine with slice-spacing of 100 to 200 µm. Drawings of the specimens were made with a camera lucida and measurements were taken with a digital caliper and rounded off to 0.1 mm. The specimens were coated with ammonium chloride prior to photographing.

Institutional acronyms: AMNH American Museum of Natural History, New York; HUJ.PAL National Natural History Collections of the Hebrew University of Jerusalem; USNM United States National Museum, Smithsonian Institution, Washington, D.C.; USGS, United States Geological Survey, Washington, D.C.; USNM and USGS numbers refer to specimens in the collection that include types and paratypes; L = maximum length; W = maximum width; T = maximum thickness; est. = estimated. All measurements in millimetres (mm).

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA Duméril, 1806
Class RHYNCHONELLATA Williams, Carlson, Brunton, Holmer and Popov, 1996
Order TEREBRATULIDA Waagen, 1883
Suborder TEREBRATULIDINA Waagen, 1883
Superfamily DIELASMATOIDEA Schuchert, 1913
Family DIELASMATIDAE Schuchert, 1913
Subfamily DIELASMATINAE Schuchert, 1913
Genus *Tunethyris* Calzada, Peybernes, Kamoun and Youseff, 1994

Tunethyris blodgetti sp. nov.
(Figs 3, 4)

Type species: *Tunethyris punica* Calzada, Peybernes, Kamoun and Youseff, 1994

Etymology: In honour of Robert Blodgett for his numerous and significant contributions to the geology of Alaska and especially to brachiopod and gastropod palaeontology.

Material examined: Thirty-nine articulated shells, of which twenty-one were measured.

Table 1

Measurements of *Tunethyris blodgetti* sp. nov. (in mm)

Specimen	Length	Width	Thickness	Apical angle°
HUJ.PAL 100.50*	23.8	17.6	11.2	79
HUJ.PAL 100.51	17.4	13.4	10.4	76
HUJ.PAL 100.52	21.6	15.0	10.5	94
HUJ.PAL 100.53	20.4	16.3	10.6	86
HUJ.PAL 100.54	18.6	10.9	9.4	82
HUJ.PAL 100.55	20.6	16.7 est.	12.5	84
HUJ.PAL 100.56	23.7	19.7	13.4	80
HUJ.PAL 100.57	24.8	20.3	11.7	74
HUJ.PAL 100.58	23.9	18.6	12.2	77
HUJ.PAL 100.59	21.9	15.3	11.5	82
HUJ.PAL 100.60	15	12.6	7.6	73
HUJ.PAL 100.61	19.3	14.8	9.6	90
HUJ.PAL 100.62	19.9	13.6	10.9	75
HUJ.PAL 100.63	19.7	16.2	10.7	75
HUJ.PAL 100.64	18.2	16.3	9.6	90
HUJ.PAL 100.65	15.9	11.2	7.8	85
AMNH FI-107783	18.4	14.2	9.4	100
AMNH FI-107784	13.2	11.9	12.0	95
AMNH FI-107785	19.3	14.6	9.2	89
AMNH FI-107786	14.2	12.9	5.9	104
AMNH FI-107787	14.6	11.6	6.3	84

.* Holotype

Types: Holotype, HUJ.PAL100.50; paratypes, HUJ.PAL51–84; AMNH FI–107783–107787.

Type locality: The shells were collected from a fossiliferous limestone and shale unit, on top of a ridge, 147 m above the base of the type section in the middle part of the Fossiliferous Limestone Member, Saharonim Formation (Anisian–Ladinian), Makhtesh Ramon, southern Israel (subunits 12–15, 31, 42) and 44 (subunit 44 occurs near the base of the Limestone and Marl Member of the Saharonim Formation). The Israel grid coordinates are 13838/99966; GPS N 30.58587497°, E 34.87624599°.

Diagnosis: Subovate to subpentagonal in outline, loop acuminate, anterior commissure very strongly sulciplicate, no transverse band present, divergent dental plates, shell smooth, lacking radial ornamentation and growth lines.

Description: The shells are small to medium-sized (Table 1), ventribiconvex, subovate to subpentagonal in outline. Ventral valve strongly convex in lateral profile, becoming more so posteriorly. Dorsal valve lateral margins slope steeply, ventral valve lateral margins almost flat; umbonal region moderately convex. In lateral profile dorsal valve slightly convex posteriorly but smoothing out to almost flat anteriorly. Apical angle ranges from 73° to 104° with an average of 80.6°. Maximum width in most shells is attained at about mid-length, but can vary either slightly toward the anterior commissure or toward the umbo. Anterior commissure strongly sulciplicate with the fold commonly long, extend-

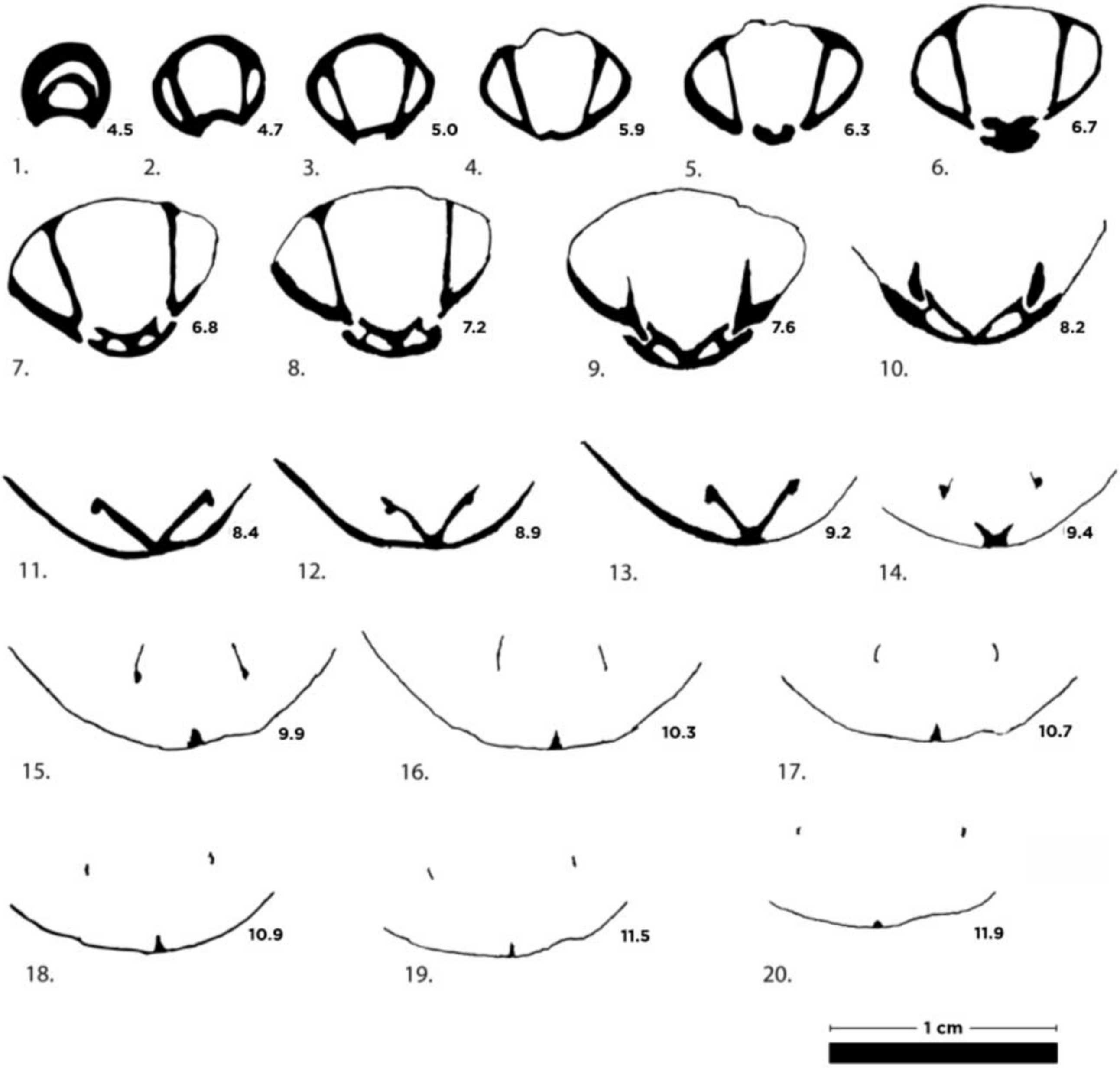

Fig. 3. Transverse serial sections of *Tunethyris blodgetti* sp. nov. paratype, Subunit 44, HUJ.PAL 100.55. Numbers show distance in mm from the umbo.

ing more than halfway toward the beak region whereas the sulcus is deep, but shorter. Lateral commissure nonsinusate, ornamentation lacking, surface smooth without colour bands. Beak short, suberect; foramen small, round, mesothyrid, nonlabiate; slightly concave symphytium rarely present; beak ridges weak.

Strong dental plates long, slightly divergent; teeth cyrtomatodont; septalium on valve floor, wide and shallow; circular pedicle collar (Figs 3, 4) the loop widens anteriorly indicating that it was long, acuminate, with the ascending parts broken off and rudimentary descending lamellae extending anteriorly from the crura, probably forming an echmidium. There is no evidence that the descending lamellae were in any way supported and no indication of a transverse band. The ascending lamellae of the homeomorph *Dielasma* are very fragile and usually destroyed during fossilization (Hall and Clarke, 1894). Inner hinge plates united with low, weak, short median septum posteriorly. No cardinal process observed.

Remarks: In general, Palaeozoic dielasmids tend to have anterior commissures that are closer to rectimarginate than sulcate. As one progresses up into the Mesozoic, sulcation tends to become more pronounced; however, the new species described in this study has a very strongly sulciplicated anterior commissure, seen in only *Tunethyris punica* from the Triassic of Tunisia. Further study will help determine whether this is due to environmental factors or evolutionary trends.

The Palaeozoic genus *Dielasma* can easily be mistaken for the Triassic *Tunethyris*, since they have a similar exter-

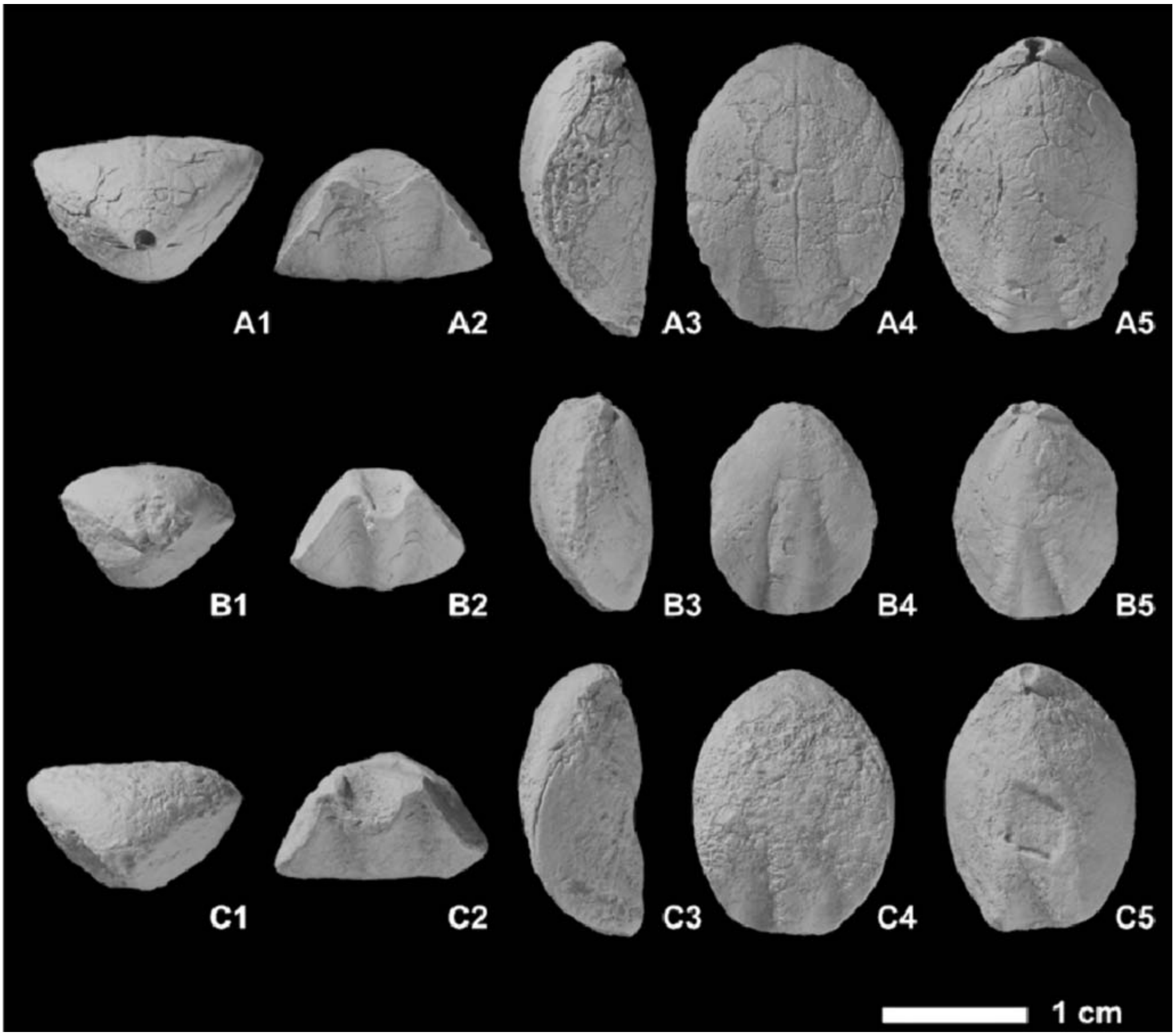

Fig. 4. *Tunethyris blodgetti* sp. nov. **A1-5.** HUJ.PAL 100.50, posterior, anterior, lateral, ventral, dorsal views, holotype; **B1-5.** HUJ.PAL 100.51, posterior, anterior, lateral, ventral, dorsal views, paratype; **C1-5**. HUJ.PAL 100.52, posterior, anterior, lateral, ventral, dorsal views, paratype.

nal anatomy and are thus homeomorphs. Smirnova (2007) described three species of *Dielasma* from the eastern Russian Platform, Kirov region (Guadalupian). *Dielasma robustum* differs in its thick, strongly inflated, equibiconvex valves and coarse growth lines that become rugae anteriorly. The apical angle ranges between 60°–65°. Internally the shells differ in that *Tunethyris robustum* has denticles on the inner and outer surface of the hinge teeth and the wide septalium rests on the valve floor unsupported by a median septum. *Dielasma kirillowense* differs from *Dielasma blodgetti* sp. nov.in its apical angle ranging between 60°–66°, gently arched pedicle collar and hook-shaped teeth with inner and outer denticles. In addition, the inner hinge plates rest on the valve floor without forming a septalium. *Dielasma subelongatum* differs in its large pedicle foramen, apical angle of between 80°–85°, strongly arched pedicle collar and massive hinge teeth.

Stehli (1956) described *Dielasma elongatum* from the Permian Zechstein Group, near Possneck, Thuringia, Germany, and the Middle Permian of Texas, which differs in its distinctly pyriform outline, mildly uniplicate anterior commissure, conjunct deltidial plates, permesothyrid pedicle foramen and sinusate lateral commissure. Further, the cardinal plate of *Dielasma elongatum* is divided into two discrete plates, extending to the valve floor, and there is an indication of a very short septalial-like structure posteriorly. King (1850) referred to this structure as a sternum-like process, supported by a medio-longitudinal plate. In addition, a small and imperfectly developed cardinal process is evident. Brugge (1974) described *Dielasma elongata* from the Permian Zechstein Group and noted that it is the only species of the genus *Dielasma* King in the Germanic Zechstein. The shells are uniplicate and almost elliptical, with a wide and deep septalium sitting on the valve floor.

Cooper (1957) described *Dielasma rectimarginatum* from the Permian of central Oregon (USNM 125414) that differs from *Tunethyris blodgetti* sp. nov. in its rectimarginate anterior commissure, very faint sulcation on some ventral valves and almost flat lateral profile.

Cooper and Grant (1976) described a suite of *Dielasma* from the Permian Glass Mountains of west Texas, in which they erected twenty-five new species. The present author will compare those taxa that are important in differentiating *Tunethyris blodgetti* sp. nov. from the Glass Mountain specimens, omitting a discussion of the uncommon forms. *D. adamanteum* (USNM 153300c) is rhomboidal in outline and has much sharper beak ridges that indicate a resemblance of the ventral valve to *Cryptonella*. The anterior commissure is not plicated, but rather has a smooth, rounded fold that Cooper and Grant (1976) referred to as a "wave." *Dielasma bellulum* (USNM 153305a) can be differentiated by its distinctive labiate pedicle foramen and most significantly, has fine, elevated radial costellae on the exterior of both valves. This feature is not evident in any other dielasmids from the Glass Mountains. *Dielasma compactum* (USNM 154260a) is more strongly ventribiconvex, has a labiate foramen and a low, narrow fold on the anterior commissure. Cooper and Grant (1976) noted that the species is unlike any other species, described from either the Glass Mountains or Guadaloupe Mountains, in that it is distinctive in its softly rounded contours and "plump" valves. *Dielasma cordatum* (USGS 118576) is pyriform in outline and has a deeply indented anterior commissure. *Dielasma ellipsoideum*ang1033 (USNM 153314c) tapers both anteriorly and posteriorly and is rhomboidal in outline with a uniplicate anterior commissure. *Dielasma expansum* (USNM 153316b) is elongate with almost parallel lateral extremities, a labiate pedicle foramen and very weak sulcus. *Dielasma pictile* (USNM 153327a) has more rounded lateral extremities and differs from *Tunethyris blodgetti* sp. nov. in its anterior commissure, which is wave-like. *Dielasma prolongatum* (USNM 118575) is distinctive in its large size for the genus, very deep dorsal valve and sulcate, narrowly folded, anterior commissure. *Dielasma pygmaeum* (USNM 153335a) is the smallest of the dielasmids described by Cooper and Grant (1976), ranging in size from 6.2–9.8 mm in length. The anterior commissure is uniplicate, with a poorly developed ventral sulcus. *Dielasma rigbyi* (USNM 153453b) is very similar to *Dielasma pygmaeum* in size, but differs in its shallower dorsal valve and less labiate pedicle foramen. The anterior commissure is strongly uniplicate. *Dielasma subcirculare* (USNM 153338a) differs in its subcircular outline and rectimarginate anterior commissure. It is a rare species, but very distinctive. *Dielasma sulcatum* (USNM 118577) differs in its pentagonal to rhomboidal outline, with a deeply uniplicate anterior commissure. *Dielasma uniplicatum* (USNM 154379) differs in its lack of sulciplication, broadly round dorsal valve, showing no evidence of fold except at anterior commissure, where the fold is very gently uniplicate. *Dielasma zebratum* (USNM 153342b) differs in its weak dorsal fold that does not involve the dorsal valve except at the anterior commissure and, epithyrid pedicle foramen, which is strongly labiate. Cooper and Grant (1976) noted that the lower lip extends in a narrow curve over the posterior of the dorsal valve in a strong pout, such that the lip barely truncates the apex of the symphytium. They further note that this throws the actual foramen into an epithyrid position.

Tunethyris blodgetti sp. nov. is similar to *Tunethyris punica* described by Calzada *et al*. (1994) from the Triassic of central Tunisia in its medium size, sulciplicate anterior commissure, and short, suberect beak. It differs in its less divergent dental plates, subovate to subpentagonal outline, ventribiconvex valves and a weaker median septum that lies on the valve floor. The septalium in *Tunethyris punica* is supported by a strong median septum. The apical angle of *Tunethyris blodgetti* sp. nov. averages 80.6°, whereas in *Tunethyris punica* it ranges from 50° to 80°.

The shells of *Tunethyris blodgetti* sp. nov. are similar to *Rhaetina*, but have well developed dental plates, a feature not found in that genus. The new species differs from Bittner's (1890) Triassic (Alps) *Tibetothyris julica* in its subovate to subpentagonal outline; *Tibetothyris julica* is distinctly oval in outline and has fine growth lines, whereas *Tunethyris blodgetti* sp. nov. lacks growth lines and radial ornamentation. In addition, *Tunethyris blodgetti* sp. nov. has more strongly divergent dental plates.

Smith (1927) illustrated *Dielasma chapini* from the Yukon Valley, Alaska (pl. 102, figs 4–6) that differs in its strongly arched dorsal valve and subovate to almost diamond-shaped outline. *Dielasma hamiltonense* from Kupreanof Island, Alaska, is similar to *Tunethyris blodgetti* sp. nov., but differs in its smaller size and less robust plications. *Dielasma liardense* from British Columbia differs in its subovate to round outline and three low plications at the anterior commissure that extend posteriorly for only about one-third of the valve length. *Dielasma iulicum* (Gyalog *et al*., 1986, pl. 10, fig. 1A–C) differs in its rectimarginate anterior commissure, subovate outline and more inflated (biconvex) valves.

Jin and Sun (1976) illustrated *Tibetothyris julica* from the Mount Jolmo Lungma region, Tibet. The serial sections of *Tibetothyris julica* show a septalium and crural bases, supported by a low septum, rather than resting on the valve floor, as in *Tunethyris blodgetti* sp. nov. *Terebratula julica* further differs from the new species in its pentagonal outline. *Tibetothyris depressa*, also illustrated by Jin and Sun (1976), differs in the presence of a small, knob-like cardinal process and its wider septalium, also supported by a low median septum, rather than resting on the dorsal valve floor. *Tibetothyris depressa* is quite different in lateral profile, where both valves are almost flat and, in plan view, the outline is sharply pentagonal. Furthermore, the foramen is permesothyrid, dental plates thin, cardinal process low with fine longitudinal grooves with a much wider and lower septalium.

DISCUSSION

Palaeoecology

The shells were collected from the beds within subunits 12–15, 31, 42 and 44 of the Saharonim Formation. The fossils generally weather out from the matrix and can easily be

Table 2

Faunal constituents of the Fossiliferous Limestone Member, Saharonim Formation (upper Anisian–lower Ladinian), Makhtesh Ramon, southern Israel (modified from Feldman 2005)

Microfossils

Conodonts:
- *Pseudofurnishius murcianus* van den Boogaard
- *Lonchodina mulleri* (Tatge)
- *Enanthiognathus ziegleri* (Diebel)
- *Hibbardella magnidentata* (Tatge)
- *Hindeodella* sp.

Ostracods:
- *Reubenella avnimelechi* (Sohn)

Foraminifera:
- Indet. Miliolids

Megafossils

Encrinus sp.
Coenothyris oweni Feldman
Tunethyris blodgetti sp. nov.
Lingula sp.
Menathyris wilsoni Feldman
Leda cf. *fibula* Mansuy
Palaeoneilo elliptica Goldfuss
Elegantina elegans (Dunker)
Myophoria germanica Hohenstein
Costatoria coxi Awad
C. multicostata Xu
Neoschizodus laevigatus Ziethen
Myophoriopsis cf. subundata (Schauroth)
Pseudoplacunopsis fissistriata (Winckler)
P. cf. *ostracina* Schlotheim
Placunopsis cf. *flabellum* Schmidt
Ostrea montiscaprilis Klipstein
Modiola cf. *raibliana* Bittner
M. cf. *salzstettensis* Hohenstein
Cassianella cf. *decussata* (Münster in Goldfuss)
Cassianella spp.
Gervillia joleaudi (Schmidt)
G. aff. *alberti* Aggasiz
G. cf. *bouei* Hauer
Plagiostoma striatum (Schlotheim)
Lima sp.
Mysidioptera cf. *vixcostata* Stoppani
Entolium discites Schlotheim
P. albertii Goldfuss
Schafhautlia aff. *mellingi* (Hauer)
Anodontophora munsteri Patte
Pleuromya cf. *mactroides* Schlotheim
Naticopsis sp.
Zygopleura spp.
Omphaloptycha sp.
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
Eoprotrachyceras curionii (Mojsisovics)
Protrachyceras cf. *ladinum* (Mojsisovics)
Protrachyceras cf. *hispanicum* (Mojsisovics)
Protrachyceras cf. *mascagnii* Tornquist
Proarcestes sp.
Monophyllites cf. *sphaerophyllus* (Hauer)
Hybodus sp.
Nothosaurus spp.
Palcodus sp.
Psephosaurus picardi Brotzen
Psephosaurus spp.

picked up on top of each bed in a systematic manner. Of course, additional material is encased within the beds and cannot be easily extracted since the shells are not silicified. These beds all contain the brachiopod *Coenothyris oweni* and share similar faunal constituents (Feldman, 2002, 2005; herein Table 2). The brachiopods are a minor, but significant component of the assemblage.

Druckman (1974b) suggested that cyclic alternation of fossiliferous limestone and shale layers on a metre 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. He further noted 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 the normal wave base (at a palaeolatitude of within 10°N) and may have been deposited even at a depth of between 100 to 200 m.

The presence of the ammonoid *Monophyllites* in the Fossiliferous Limestone Member of the Saharonim Formation indicates a deep ocean environment, according to Westermann (1996). However, the marine Middle Triassic series of Israel belongs to the Sephardic Province, which sharply differs in its cephalopod composition from coeval “normal” or Panthalassan faunas (Feldman, 2005). Extreme abundance and diversity of nautiloids as in the Triassic of Israel is diagnostic of relatively shallow marine environments up to 200 m in depth, according to Bucher (pers. comm., 1996); this conforms to Druckman’s (1974b) thoughts on depth. 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. Triassic phylloceratids, such as *Monophyllites* are not, according to Bucher, indicative of deep water, but are generally ubiquitous in ammonoid-bearing beds.

The depositional environment of the Saharonim Formation was in an open shelf environment of quasi-normal salinity, a carbonate sequence with shale, marl and evaporite interbeds that represents the main transgressive phase of the Middle Triassic in the region (Benjamini *et al*., 2005). The host rock lithology of the brachiopod-bearing beds is similar to the host rock lithology at Felsőörs, Balaton Highland, Hungary, where a finer-grained limestone grades into marlstone in places, indicating a lower-energy regime (Pálfy, 1990).

The brachiopod assemblages in the Triassic of Makhtesh Ramon are similar to the fauna, described by Pálfy (1990) at Felsőörs (Anisian), in that both are low-diversity assemblages. However, whereas the associated megafauna at Felsőörs is sparse, consisting only of crinoid ossicles, the megafauna in the Saharonim Formation is extremely diverse (see Table 2). Another difference between the Felsőörs depositional environment and that of the Saharonim

Formation is that at Felsőörs the water was quiet with a scarcity of hard substrates and limited nutrient supply, but otherwise stable conditions (Pálfy, 1990). This author considers the palaeocommunity at Felsőörs to be adapted to an unusual setting, since the brachiopod species are not represented at many other localities worldwide.

In summary, the present author concurs with Druckman's (1974b) interpretation that most of the Lower Saharonim Member was deposited at least beneath normal wave base and may have been deposited even at a depth of between 100 to 200 m. In addition, the depositional environment of the Saharonim Formation was in an open shelf environment of quasi-normal salinity that represents the main transgressive phase of the Middle Triassic in the region as per Benjamini *et al.* (2005). In addition, the great abundance and diversity of nautiloids in the Triassic of Israel strongly indicates a depositional environment that was shallow marine.

Palaeobiogeography

The Saharonim Formation shows affinities to the Germanic Muschelkalk in that it consists primarily of fossiliferous, bioturbated, and stromatolitic limestones, marls, minor shales, occasional sandstones with plant remains and reptile bones, lithographic limestones with fish remains and occasionally gypsum intercalations (Hirsch, 1992; Feldman, 2005).

Vertebrate remains found in the Saharonim Formation, although not in the same stratigraphic horizon as *Tunethyris blodgetti* sp. nov., include the fish *Hybodus* and the marine reptiles *Nothosaurus, Placodus,* and *Psephosaurus* (see Table 2). The Sephardic Province (Hirsch, 1972) Muschelkalk facies contains the following endemic taxa: *Pseudofurnishius murcianus, Sephardiella mungoensis* (conodonts), *Gevanites epigonus, Israelites ramonensis, Protrachyceras hispanicum* (ammonites), *Myophoria coxi, Gervillia joleaudi* (bivalves). According to Hirsch (1992), their ecological analogues and stratigraphic equivalents in the Germanic Muschelkalk are endemic neogondolellid conodont and ceratidid ammonite taxa and 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). The Sephardic Province is characterized by a fauna of restricted Tethyan nature and overwhelmingly endemic (Hirsch, 1990). As the Tethys widened during the Ladinian stage, the distinctive Sephardic Province developed on the southern epicontinental Tethyan shelf (Hirsch, 1992). The presence of endemic species of the brachiopod *Coenothyris oweni* (Feldman, 2002, 2005) in southern Israel is useful in differentiating the Sephardic Province from the Germanic Muschelkalk and the Tethyan realm faunas to the north (for a discussion of the stratigraphic distribution of *Coenothyris* see Usnarska-Talerzak, 1990).

According to Halamski *et al.* (2015), Ladinian (Late Middle Triassic) brachiopods are poorly known. They describe a highly endemic Ladinian brachiopod fauna from Mt. Svilagja in Dalmatia and list worldwide Ladinian brachiopod faunas (see Halamski *et al.*, 2015, p. 570). Ke *et. al.* (2016) reported a dip in brachiopod diversity during the Ladinian; however, see Torti and Angiolni (1997) for a systematic description of 17 Ladinian brachiopod taxa from Val Parina, Bergamasc Alps, northern Italy. The specimens collected at Makhtesh Ramon will help fill the gap in our knowledge of these faunas as well as the apparent gap in the Ladinian of the northern Caucasus (Ruban, 2006).

In the Late Triassic, brachiopod faunas became more abundant, increasing steadily from the Carnian through the Rhaetian, with species quantity increasing more than threefold in the Norian (Ruban, 2006; Ke *et al.*, 2016). Detre (1993) listed abundant Carnian brachiopods from the southern and northern Bakony Mountains, the Iszkahegy, the Vértes Mountains, the Buda Mountains, the Triassic blocks east of the Danube, and the Bükk Mountians. Sandy and Stanley (1993) noted that Smith (1927) incorrectly referred to some rhynchonellids from the Triassic of the western Cordillera of North America, specifically *Dielasma*, (originally cited in Ager and Westermann, 1963) to species described from Europe. The only dielasmid genera that morphologically resemble *Tunethyris* in the Late Triassic are: *Adygella*, *Apsidothyris, Whitspakia*, *Rhaetina* and *Pseudorhaetina*. There is no recorded occurrence of any other brachiopod genus in the Late Triassic that can be mistaken for either *Dielasma* or *Tunethyris*.

Sandy and Stanley (1993) discussed the difficulty in interpreting the presence of Late Triassic invertebrate groups from the Tethyan of Europe as well as some displaced terranes from North America. Stanley *et al.* (1994) noted the presence of *Pseudorhaetina antimoniensis* and *Spondylospira lewesensis* in the Late Karnian to Norian of the Antimonio Formation of Mexico, in association with a carbonate-bearing interval with a shallow-water, normal marine fauna. Some of the brachiopod species from the Luning Formation, Nevada, are typical of the Rhaetian Reef Limestone, Kössen Beds, and Dachstein Limestone of Austria and southern Germany (see Stanley *et al.*, 1994). They note that there are earlier occurrences of some species in North America and propose five hypotheses to explain this enigma (see Sandy and Stanley, 1993, p. 448). They proposed that the Hispanic Corridor, an immature seaway connecting the western Tethys with eastern Panthalassa, may have been open sporadically during the Late Triassic (Smith, 1983; Smith *et al.*, 1990; Stanley, 1994). The occurrence of cold-seep brachiopods could explain the disjunctive distribution of "typically Tethyan" brachiopods in distribution and that the association of these brachiopods with chemosynthetic communities may indicate that the distribution of these taxa may not have any latitudinal control (Sandy, 1995). Examples of brachiopod taxa that fall into this category from the Late Triassic include *Carapezia* and *Rhynchonellina*. According to Sandy and Stanley (1993), the Hispanic Corridor may have been open in the Late Triassic, during which time brachiopod taxa could have utilized this route to move between faunal realms. In fact, they proposed that the fauna of the Nevadan Paradise terrane that existed during the Late Triassic may shed light on the geography of the region.

Sandy and Aly (2000) described a Norian brachiopod fauna from the United Arab Emirates that includes *Misolia*, *Spiriferina* and *Hagabirhynchia*. Eleven species of Rhaetian brachiopods from Iran were described by Kristan-Tollmann *et al*. (1979) and Sandy (1994) described ten species of Norian brachiopods from the Pucará Group of central Peru.

It should be noted that in the Late Triassic (specifically across the T-J boundary), there were significant changes to the marine benthic ecosystem that had implications for ecosystem functioning (Barras and Twitchett, 2016). They noted a reduction in burrow diameter of tracemakers as well as a reduction in diversity and maximum burrow depth. In the Late Triassic, significant biotic decline, along with substantial Rhaetian regression, may have affected the abundance and distribution of brachiopods (Tanner *et al*., 2004). Ke *et al*., (2016) reported that global brachiopod diversity changes from Late Permian through the Triassic were mainly influenced by palaeoclimate changes or, as they stated, a palaeoaltitude-related thermal gradient that was the main controlling factor for the spatial distribution of brachiopods in the Triassic.

CONCLUSIONS

Thirty-nine specimens serve as the basis for erecting a new species of a dielasmid brachiopod from the Triassic of southern Israel. The shells are smooth, lacking radial ornamentation and growth lines and are subovate to subpentagonal in outline. The loop is acuminate with no transverse band evident and the anterior commissure is very strongly sulciplicate. The dental plates are divergent.

The shells were collected from the marine Middle Triassic series of Israel that belongs to the Sephardic Province (Feldman, 2005). Extreme abundance and diversity of nautiloids, as in the Triassic of Israel, is diagnostic of relatively shallow marine environments. 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. Differences between the Sephardic Province faunas can be recognized on the southern margin of the Tethys shelf and the Germanic (= Muschelkalk) Province and Tethyan Realm faunas to the north.

The brachiopod assemblages in the Triassic of Makhtesh Ramon are similar to the Anisian fauna described by Pálfy (1990) at Felsőörs, in that both are low-diversity assemblages. The latter author believed that the palaeocommunity at Felsőörs was adapted to an unusual setting, since the brachiopod species are not represented at many other localities worldwide.

Ladinian (late Middle Triassic) brachiopods are not well known and there seems to be a decrease in their abundance and diversity during that time period. The specimens collected in Israel will help fill the gap in our knowledge of these faunas. In the Late Triassic, brachiopod faunas became more abundant, increasing steadily from the Carnian through the Rhaetian.

It is difficult to interpret the presence of Late Triassic invertebrate groups from the Tethyan of Europe as well as some displaced terranes from North America. Stanley *et al*. (1994) noted that there are earlier occurrences of some species in North America and proposed five hypotheses to explain this enigma (see Sandy and Stanley, 1993, p. 448).

In the Late Triassic, there were important changes to the marine benthic ecosystem that had implications for ecosystem functioning. At that time, a major biotic decline, along with a substantial Rhaetian regression, may have affected the abundance and distribution of brachiopods.

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