THE RAMONALINIDS: A NEW FAMILY OF MOUND-BUILDING BIVALVES OF THE EARLY MIDDLE TRIASSIC

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Abstract: *Ramonalina* n. gen. is a large thick-shelled bivalve abundant in mounds preserved in the Gevanim Formation (late Anisian, Middle Triassic) of southern Israel. This bivalve was an edgewise-recliner with a flattened anteroventral (functionally basal) surface and partially fused valves. It is the basis of a new family, the Ramonalinidae, which is descended from the myalinids through adaptation to edgewise positioning. Ligamental attachment was inadequate to hold valves together on large adults, resulting in valve displacement followed by shell secretion in the apical area that fused valves together and caused irregular growth on abapical areas. The ramonalinids formed large, nearly monospecific mounds on firm mud substrates in shallow marine waters. These are the largest Middle Triassic bivalve mounds known.

**Key words:** Middle Triassic, Bivalvia, systematics, Israel, mounds.

LARGE myalinid bivalves are a characteristic part of the marine recovery biota that appeared after the great end-Permian mass extinction event (Schubert and Bottjer 1995; Krystyn *et al.* 2003) and contrast with the small, dwarfed or thin-shelled condition of other basal Triassic taxa (Hautmann and Nützel 2005). Large and thick-shelled myalinid bivalves occur in thick shell beds with few other taxa in basal Triassic deposits (Krystyn *et al.* 2003; Birkenmajer 1977). This tendency to occur in shell bed accumulations or mounds is similar to occurrences of Carboniferous/Permian myalinids, suggesting that they were little affected by the end-Permian extinction. Prominent shell beds of basal Triassic myalinids are known from regions as diverse as the Boreal Province in Svalbard (Birkenmajer 1977), the Great Basin of western North America (Boyer *et al.* 2004) and the north margin of Gondwana in the Tethyan Province (Krystyn *et al.* 2003). Most of these basal Triassic myalinids are placed in the genus *Promyalina*, one of two myalinid genera known to occur in the Early Triassic (McRoberts 2005).

As biotic diversification proceeded during the Triassic, myalinids became a minor part of the marine biota, and they disappeared by the end of the Early Triassic (McRoberts 2005). However, myalinids contributed to the Triassic diversification event by giving rise to a specialized lineage of myalinid-derived winged edgewise recliner (i.e. reclining with the commissure plane more or less perpendicular to the substrate) descendants in the early Middle Triassic. These Middle Triassic edgewise recliners appeared in the late Anisian on the north edge of Gondwana. The environmental preferences and general mode of occurrence of this new group were similar to that of the myalinids, but the new group acquired distinctive new characters and achieved a mound-building capability greater than that of their ancestors and comparable to that of coeval corals and calcareous sponges.

GEOLOGICAL SETTING

The Ramonalinidae, new family, including *Ramonalina* nov. gen., is erected to include a lineage of bivalves known from the central Negev Desert of southern Israel (Text-fig. 1). These occur in great abundance in strata exposed at Makhtesh Ramon (*makhtesh* is a term for a basin-like erosional feature in the centre of a doubly plunging anticline; see Avni 2001) within shell beds composed dominantly of these bivalves. The main occurrence is in a unit locally called 'The *Myalina* Reef' that occurs near the top of the Upper Member of the Gevanim Formation (Text-fig. 2). This interval contains mounds of several metres thick and composed of great numbers of the species *Myalina ramanensis* Brotzen, 1956. The mounds containing *M. ramanensis* occur in Unit 40 of the Upper Member of the Gevanim Formation as described by Druckman (1974) and earlier named Unit

TEXT-FIG. 2. The '*Myalina* Reef' unit of the Gevanim Formation at its westernmost exposure, Har Gevanim, Negev Desert, Israel.
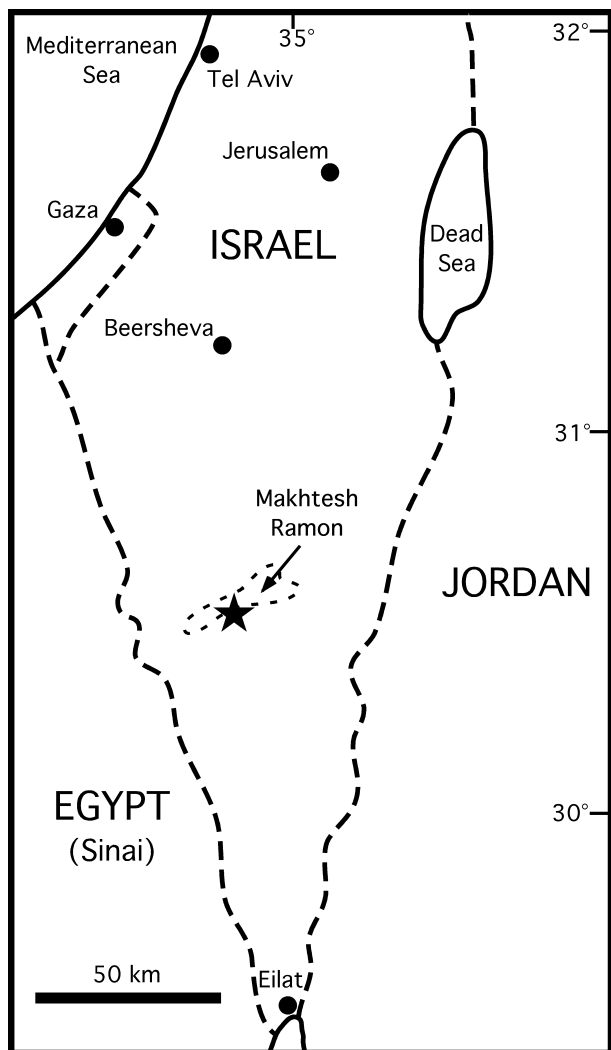
TEXT-FIG. 1. Locality map showing the location of Makhtesh Ramon in the Negev Desert of southern Israel.

C2a by Brotzen (1956). Unit 40 is truncated in the east and west by faults, and thus it has only 2.5 km of exposure. It thickens and thins along the Gevanim Valley where it is exposed, being 6.8 m thick at its easternmost location in the valley and 4.5 m thick at its westernmost exposure. At one point in this exposure, the unit is reduced to a thin dark-coloured shelly horizon only a few centimetres thick, and then rapidly thickens laterally. The Upper Member of the Gevanim Formation contains a mix of yellow sandstones, siltstones, shales and thin limy beds that contrast with overlying and underlying shale and carbonate dominated intervals containing a diverse normal marine biota. The Gevanim Formation is underlain by the Ra'af Formation and overlain by the Saharonim Formation; all three units are part of the Ramon Group (Zak 1963). The Gevanim Formation is exposed only in the central Negev, but age-equivalent strata are exposed in the Sinai about 45 km to the south-west (Lerman 1960; Druckman 1974; Eicher and Mosher 1974). The Gevanim Formation contains palynomorphs that indicate a placement within the *Accintisporites ligatus* zone (Horowitz 1970), and the Upper Member of the Gevanim Formation contains conodonts and ostracodes that indicate a Late Anisian age (Hirsch and Gerry 1974; see also Benjamini *et al.* 1993, fig. 2).

The sands and sandy mudstones of the Upper Member of the Gevanim Formation indicate deposition in shallow waters in a nearshore setting; part of the regressive interval identified by Brotzen (1956). He considered the '*Myalina* Reef' to be deposited during a subsequent transgression, but the '*Myalina* Reef' is overlain by plant-bearing sands and is more reasonably considered as part of the regressive interval. Except for bivalves in the mounds and common plant fossils in the sandstones, the Upper Member of the Gevanim Formation has a sparse fossil biota, but this is probably a result of carbonate dissolution in the siliciclastic sediments. More calcareous strata above and below the '*Myalina* Reef' bed contain a diverse marine biota (Druckman 1974; Benjamini *et al.* 1993).

The specimens of *M. ramanensis* used for descriptive documentation in this study are from a site about 640 m east of the peak of Har Gevanim (Mount Gevanim), on its south-facing slopes (30°35.224′ N, 34°53.261′ E), the same location as that of the type specimen of *M. ramanensis* collected by Brotzen (1956). This location is marked by a series of small orange signs placed by the Geological Survey of Israel describing the stratigraphic units and indicating their boundaries. The shell accumulations that form mounds are dark-coloured and contrast with the lighter-coloured siliciclastic units above and below. The centre portions of mounds are often cemented and produce lithified rock masses, but at some places

lithification is minor and shells weather out into talus piles of loose specimens and shell fragments. Within the shell beds, most of the bivalves are articulated and occur in life position with their plane of commissure oriented perpendicular to bedding.

Petrographic analysis of the *M. ramanensis* mound rock shows that it is an argillaceous limestone in most areas of exposure. The component shells are embedded within a mud matrix that is cemented with carbonate, consisting of large crystal units within the interior of shells and as finer cement outside the shell. Empty shell interiors and other shelter voids are filled with coarse spar. Some of the mud matrix and geopetal fills were later partially phosphatized. The mud matrix contains much yellowish brown clay and silt, but by volume it is dominantly carbonate, indicating rapid cementation of the clay before compaction. The matrix contains abundant small bivalves and bivalve bioclasts and some ostracode microfossils. At the margin of mounds, the 'Myalina Reef' bed extends out as a thin dark-coloured calcareous layer, probably produced by calcareous fines winnowed from the mounds (Brotzen 1956).

The palaeoenvironment of sediments of the Upper Member of the Gevanim Formation is interpreted to have been marginal marine. The unit contains a low diversity assemblage of fossils with small bivalves (unidentified), lingulid brachiopods and ostracodes found in the matrix around and inside the ramonalinid shells. Some fragments of bone (Druckman 1974) and a few poorly preserved internal molds of *Germanonautilus* nautiloids (our collections) have been recovered from the deposit as well. A few bivalves are encrusted by microconchid tubes: a group of fossils commonly found in marginal marine environments (Taylor and Vinn 2006). Thin sandstones immediately below and above the mounds contain fish and reptile bone; thicker sandstones contain common plant fossils (Brotzen 1956). The clay mud matrix around the myalinid-type bivalves and presence of cross bedding in sandstones above and below the mounds support an interpretation of nearshore or shore zone environment for this deposit. There were numerous brief transgressions and regressions over the Arabian Plate during the Middle Triassic (Sadooni and Alsharhan 2004). Sadooni and Alsharhan (2004) considered the Gevanim Formation to represent a generally regressive facies of siliciclastic units with thin shell bed limestones, such as beds containing the bivalve mounds.

Late Anisian sandstones and limestones are also exposed 45 km south-west of Makhtesh Ramon at Gebel Araif el Naga in the Sinai (Lerman 1960; Druckman 1974; Eicher and Mosher 1974). The biostratigraphically equivalent sequence is about half the thickness of the Makhtesh Ramon section and lacks the 'Myalina Reef' and associated macrofossils, but it is still part of the same regres-

sive facies (Druckman 1974; Sadooni and Alsharhan 2004).
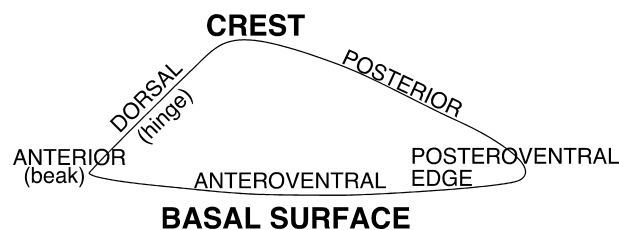
SHELL ORIENTATION

Edgewise recliner bivalves have modified the shape of their valves to produce a large flat surface that extends across the anteroventral portion of both valves, forming a surface capable of maintaining a stable orientation on the sediment surface. This surface extends from the beaks to the posteroventral margin on the valves of ramonalinids. The resulting cross section is triangular along the plane of commissure with the inclined hinge axis located along a shorter side of the triangle. This is problematic for the description of ramonalinid valves because orientation terminology (anterior, posterior, dorsal, ventral) is set by reference to the hinge axis or oral-anal axis, while the prominent shell features of these bivalves and functional life orientation is about 45 degrees away from standard biological directions. The posterodorsal end of the hinge projects as a crest that is functionally dorsal, and the flattened surface is functionally ventral as a basal surface aligned on the sediment surface. Reference to orientation using both types of criteria is needed in describing edgewise recliners, and the difference between biological and functional orientation is shown in Text-figure 3.

SYSTEMATIC PALAEONTOLOGY

Family RAMONALINIDAE fam. nov.

Type genus. *Ramonalina* gen. nov.

Diagnosis. Thick-shelled edgewise reclining bivalves with duplivincular ligament of numerous very narrow ligament grooves; valves folded in well-defined angular blunt-edged folds; anteroventral surfaces of articulated shells join to

TEXT-FIG. 3. Orientation terminology for edgewise recliner bivalves. Terms dorsal, ventral, anterior and posterior refer to biological orientation determined by reference to hinge axis. Terms in bold are relevant to discussion of life orientation, relative to resting on a horizontal sediment surface. The crest is functionally dorsal and the basal surface is functionally ventral.

form a flattened functionally ventral basal surface; valves fused at maturity.

Derivation of name. Named for the type genus.

Included genera. *Ramonalina* gen. nov.

Occurrence. Known only from the Gevanim Formation, Negev Desert, Israel, Late Anisian, Middle Triassic.

Discussion. The family Ramonalinidae is erected for a lineage of thick-shelled bivalves that possessed a dysfunctional ligament incapable of holding large shells together, resulting in frequent valve displacement and fusion of valves along the hinge line and the anteroventral margin at maturity. In size, ligament, beak structure and age of occurrence, ramonalinids reveal their myalinid ancestry, but differ from myalinids in lacking auricles, lacking a modiolid small juvenile growth stage, strong folding of valves, an excessive thickening of valves in the apical region combined with thin shell wall in the abapical regions, valve discordance produced by valve slippage and displacement and fusion of valves at maturity. The angular folding of ramonalinid valves contrasts with the low inflation of myalinid valves.

Large thick-shelled species of myalinids are more inequivalved and probably lay on one valve during life, a different life orientation than is characteristic for ramonalinids. Edgewise life orientation of large myalinids is adopted only by the middle Permian *Novaculapermia* McRoberts and Newell, 1997, a myalinid that adapted a solenoid-like life habit as an infaunal inhabitant, not a recliner. However, a myalinid ancestry for the edgewise-reclining alatoconchids (McRoberts 2005) indicates that transforming the myalinid life habit to edgewise reclining is relatively simple, requiring only a change in shell form to produce a functional basal surface. This is a large change, but not unusual during a time of adaptive radiation of marine biotas like that taking place during the middle Triassic.

Ramonalina differs greatly from other large edgewise recliners. It differs from alatoconchids in having beaks projecting anteroventrally (functionally downturned) instead of dorsoposteriorly (functionally upturned), and it lacks the wide interarea with irregular ligament grooves of *Alatoconcha* (Yancey and Boyd 1983). *Ramonalina* differs from wallowaconchids in having valve folding that does not develop wings with parallel sides, lacking chambers in the folds and in lacking the megalodontid teeth of *Wallowaconcha* (Yancey and Stanley 1999). In features of general shape, beak orientation and basal surface, there are many similarities to wallowaconchids, but hinge and wing characters are definitive for distinguishing the groups. When only shell shape is available for comparison, *Ramo-*

nalina can be distinguished from other recliner groups by the less acute condition of folding on the wings. They are folded at an angle of about 30–45 degrees and never have parallel alignment of the wing walls within the area of fold.

Genus RAMONALINA gen. nov.
Text-figures 4–8, 10–11

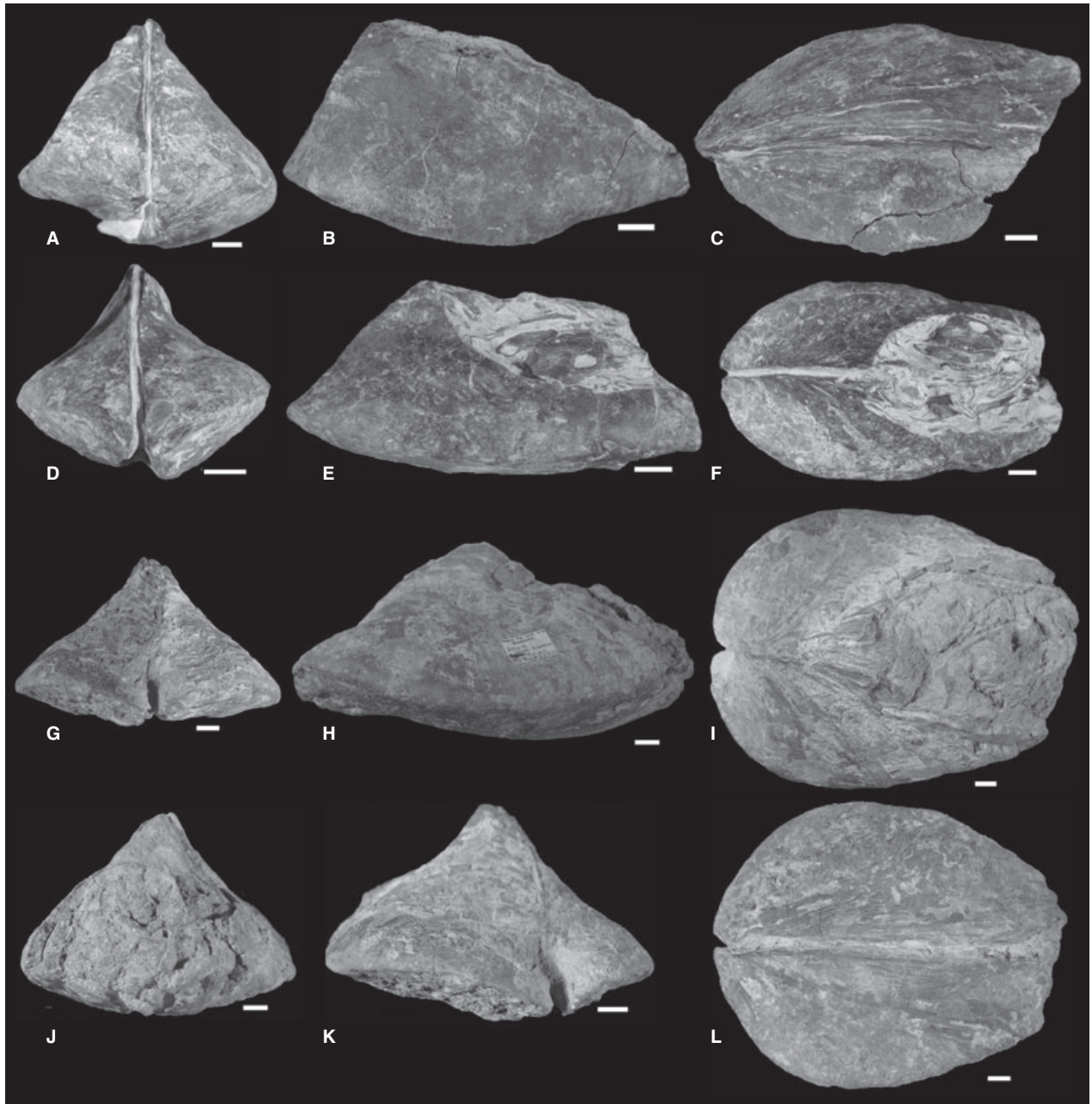*Type species.* *Myalina ramanensis* Brotzen, 1956.

Diagnosis. Large, thick-shelled and nearly equivalved edgewise recliners; valves strongly folded, producing a flattened gently curved anteroventral surface; dentition of a single ridge on the right valve and furrow on opposite valve; duplivincular ligament of numerous very narrow closely spaced ligament grooves; fusion of valve margins in apical areas occurs on mature adults; shell thickness varies from very thick (5–10 mm) in apical region to thin (1 mm) on the posterior margin.

Derivation of name. *Ramonalina* combines the name of a geomorphic feature, Makhtesh Ramon, with that of myalinids, the ancestor of the new genus.

Occurrence. Known only from the Gevanim Formation, Negev Desert, Israel, Late Anisian.

Description. Large, thick-shelled and nearly equivalved edgewise recliners; valves strongly folded, producing a flattened anteroventral surface; auricles lacking; lacking a modiolid juvenile growth stage; dentition of a single ridge on right valve and furrow on opposite valve; duplivincular ligament of numerous very narrow and closely spaced ligament grooves nearly parallel with the hinge axis; fusion of valve margins in apical areas occurs at maturity; shell thickness varies from 5–10 mm in apical region to 1 mm on the posterior margin; valves often offset before fusion; posterior margin usually lamellose and may develop a wavy, S-shaped crestline; wide-spaced small lamellae and subdued shell undulations on apical areas and more extended, irregular lamellae often developed on posterior crestline of the valves; thick secondary prismatic shell layers may be secreted on interior of valve on mature adults. The most distinctive characters are developed on mature adult shells (Text-figs 4–5).

Discussion. *Ramonalina* is erected for species of an edgewise recliner bivalve with hinge characters similar to selenimyalinids, including a duplivincular ligament consisting of many very narrow grooves aligned nearly parallel to the hinge line (Text-fig. 6A) and ridge and groove dentition and byssal groove (Text-fig. 6B), but with very thick valves and heavy infilling of apical areas that develops into fusion of valves at maturity (Text-fig. 7). Species of the genus have less strongly folded valves than

TEXT-FIG. 4. *Ramonalina ramanensis* (Brotzen, 1956). Three specimens scaled to similar dimensions for the purpose of comparison. Note valve displacement shown by offset in beaks (A, D), variation in angle of hinge axis to basal surface (B, E, H) and curvature of basal surface (B, E, H). A–C, beak, left lateral and anteroventral views, specimen NRM-PZ Mo161129. D–F, beak, left lateral and dorsoposterior (crest) views, specimen NRM-PZ Mo161128. G–L, beak, left lateral, dorsoposterior, abapical, oblique beak and anteroventral views, specimen NRM-PZ Mo152775 (holotype of *R. ramanensis*). Scale bars represent 1 cm.

alatoconchid or wallowaconchid edgewise recliners but produce thicker shells for body size than the other groups.

Shells of *Ramonalina* have a shape that can be produced by modifying a conventional myalinid shell shape to produce a flattened functionally basal surface on the anteroventral margin of the shell. The shell form of *Ramonalina* would be generated if anteroventral/posterodorsal shortening of the myalinid shell pushed the valves out into large folds. The anteroventral portion of the folds then produced a wide flattened surface for positioning on the substrate. This became a functional ventral resting surface for a life habit of living on the sediment surface as a free-living edgewise recliner. This life habit is
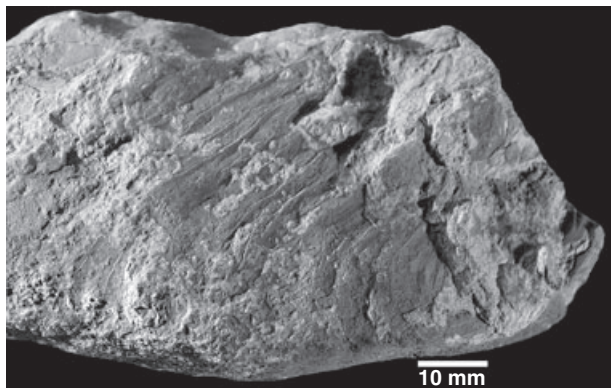
TEXT-FIG. 5. Ornamentation on *R. ramanensis* (Brotzen, 1956). Subdued lamellae and concentric shell undulations in vicinity of beak on right valve of young adult specimen. Specimen NRM-PZ Mo161131.

associated with excessive thickening of valves in the apical region combined with thin shell wall in the abapical regions, valve discordance produced by valve slippage and displacement (Text-fig. 8) and fusion of valves in adult growth stages.

The ligament of *Ramonalina* is most similar to *Selenimyalina* Newell, 1942, a genus with duplivincular ligament unlike other myalinids (Newell 1942, p. 63). Newell notes that *Selenimyalina* is similar to several species of myalinids of Triassic age and suggested that *Selenimyalina* might be unrelated to other myalinids. This suggests that *Promyalina* is descended from *Selenimyalina* and that *Promyalina* is the ancestor of *Ramonalina* (Text-fig. 9). *Ramonalina* appears at a higher level within the Triassic (late Anisian) than any known myalinid (McRoberts 2005), now that the Middle Triassic *Aviculomyalina* is excluded from the Myalinidae (Waller and Stanley 2005; McRoberts 2005). The ligament of *Promyalina* is not documented well enough to determine whether this assumption is correct, but *Ramonalina* is different from

known basal Triassic species of *Myalinella*, and it is expected that its ancestor will be found among one of the early Triassic species of *Promyalina*.

Flattening of the shell to rest on the sediment surface is responsible for the broadening of the shell and positioning the posterior end of the hinge line to form a high crest. Shells observed in life position in outcrop are separated in the sediment matrix and have limited contact with other shells (M. Wilson, pers. obs.), although growth interference by crowding is evident on some shells (Text-fig. 10). There is no evidence of attachment to hard surfaces and byssal attachment was limited to juvenile growth phases.

Ramonalina includes two described species, *M. ramanensis* Brotzen (1956) and *M. beneckei* Brotzen (1956). The latter species occurs in underlying strata of the same section. The holotype of *M. beneckei* could not be located. *M. ramanensis* differs from *M. beneckei* by being larger and having a sharper, higher crest, and both are members of the same lineage. *M. ramanensis* develops the most distinctive characters of the genus.
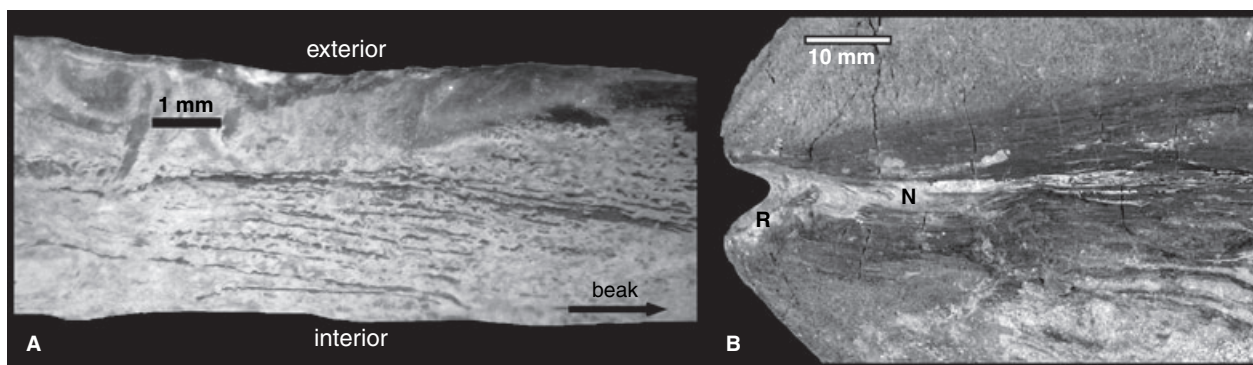
Ramonalina ramanensis (Brotzen, 1956)
#### Text-figures 4–8, 10–11

Myalina ramanensis Brotzen, 1956, p. 209, pl. 1, fig. 1C, pl. 2.

Diagnosis. Large (up to 15 cm length) shells with thickened shell walls, gently curved basal surface and strong hinge fusion, resulting in overlapping of valve margins on abapical part of basal surface and irregular posterodorsal valve margin.

Description. Shell elongate with a triangular cross section and a trigonal form in anterior view; auricles are lacking; hingeline forms a 40–60 degree angle with the basal surface; beak is small and rotated inward and slightly anteroventrally; the tip of the beak is missing on all specimens examined, but a modiolid young


TEXT-FIG. 6. Hinge characters of *R. ramanensis* (Brotzen, 1956). A, narrow, closely spaced grooves of duplivincular ligament on left valve. Specimen NRM-PZ Mo161125. B, byssal notch (N) and low ridge (R) that serves as a tooth on the beak of right valve and fits with a shallow groove on left valve. This type of ridge and groove articulation is also present on valves of *Myalina*. The byssal notch is open only on juveniles but remains visible on thickened adult shells. Specimen NRM-PZ Mo161135.
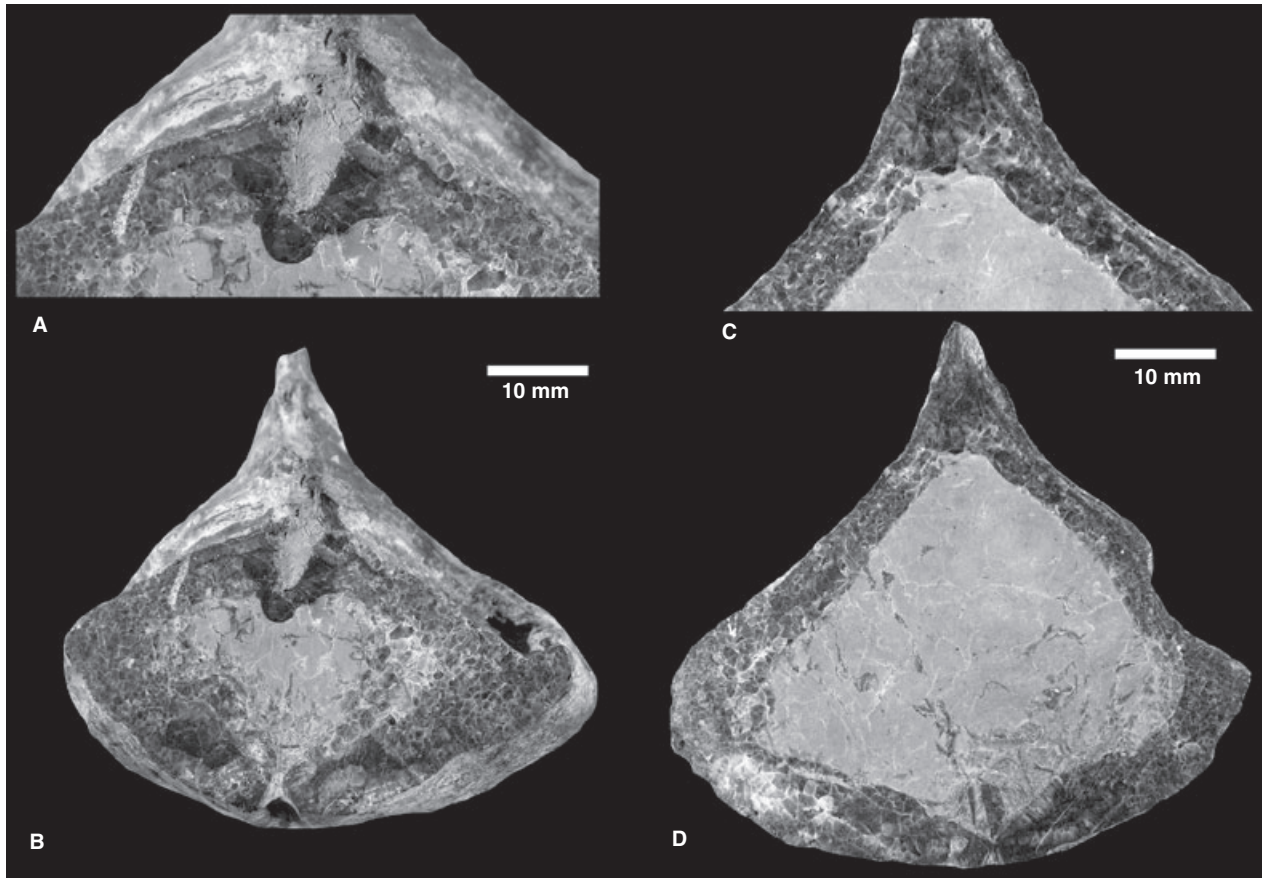
TEXT-FIG. 7. Cut sections showing secondary secretions on interior of valves and valve fusion along hingeline of *R. ramanensis* (Brotzen, 1956). A, B, section near apex of beak. The dark shell in interior is shell that has grown out around ligament field. C, D, section showing fused hinge in area near the crest. Specimen NRM-PZ Mo161130.

TEXT-FIG. 8. Valve displacement and overlap in *R. ramanensis* (Brotzen, 1956). A, displaced valves with valves displaced in anteroventral-posterodorsal direction. Specimen NRM-PZ Mo16128. B, Anteroventral margins of valves overlapping in central part of shell (right side of photo); right valve partially overlaps left valve. Specimen NRM-PZ Mo161133.
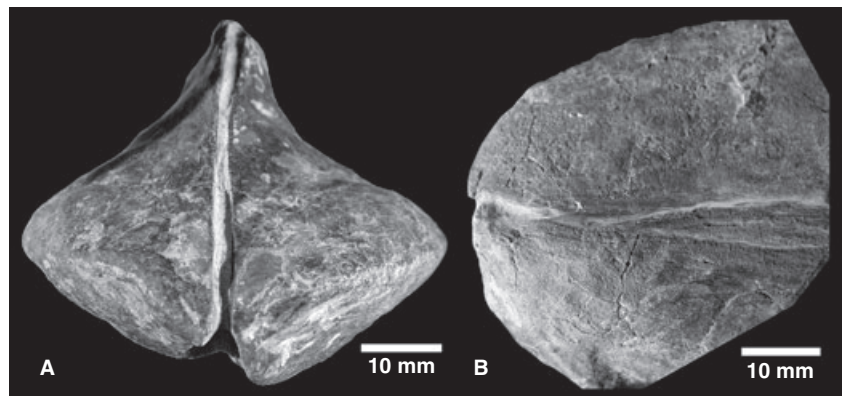
juvenile growth stage is not present; hingeline contains a narrow interarea with thin grooves of a duplivincular ligament; dentition of a tooth-like ridge on the right valve and corresponding groove on the left valve that provides some articulation for the valves and is located at the anterior end of the ligament field; juveniles with shallow byssal sinus symmetrically developed between valves near the apex, but closed off and nonfunctional on adults; shell margins along the basal surface (resting on substrate during life) are thickened; apical portions of the valves are very thick on mature specimens, while the posterior growth margin is thin shelled; subdued lamellae may be present on posterior margin of shells; shell margin from the top of the crest to the abapical edge is commonly irregularly lamellose; perhaps separated with thick conchiolin sheets; concentric undulations of the shell wall present in some specimens. Musculature and pallial features unknown.
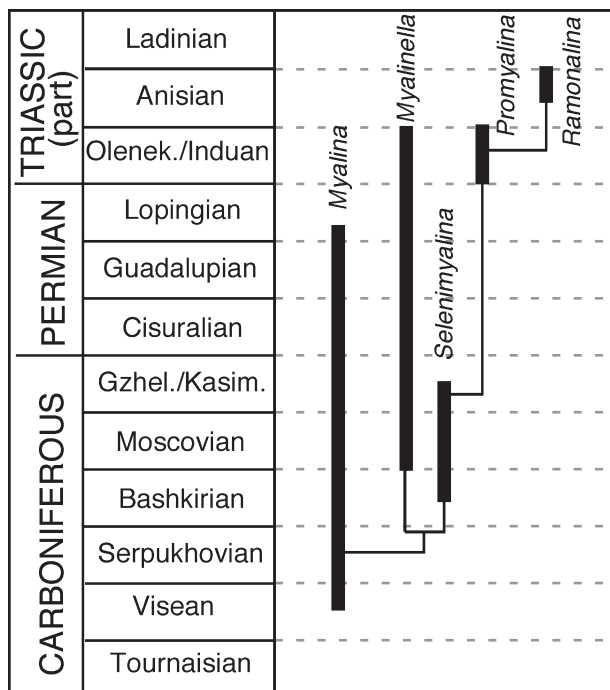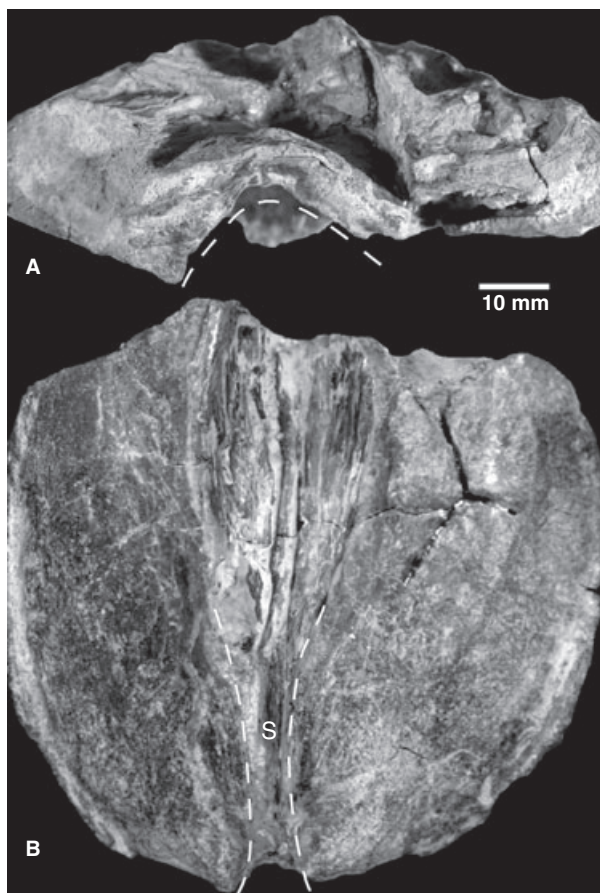
TEXT-FIG. 9. Suggested ancestor–descendent relationship of Ramonalina to myalinids. Chart adapted from McRoberts (2005).

TEXT-FIG. 10. Deformed growth in *R. ramanensis* (Brotzen, 1956). A, abapical view of broken shell, basal surface down, showing large indentation (indicated by dashed line) on basal surface of a mature specimen. Deformation caused by crowding and growth over another shell. Note the continuous shell of valves on basal surface and lack of significant fracturing in the shell on this arch. Upper surface is broken down by compaction. B, basal anteroventral view of shell, showing ovoid area of indentation (upper half of photo) and the separation of valves produced by growth interference. The dashed lines mark edge of valve before interference began, and the area marked by S is secondary shell secreted by the bivalve as valves were forced apart and shell fusion began. The dark band at letter S is a sharp ridge of secondary shell material projecting downward; also seen in A below the dashed line. Specimen NRM-PZ Mo161136.

Shell microstructure consists of a thick inner shell layer of large crystals of calcite, either as a mosaic recrystalized from aragonite or as layers of simple columnar calcite prisms with diameters of 50–100 μm (Text-fig. 11D–F) and an outermost thin dark-coloured layer of smaller prisms with diameters of 20–30 μm (Text-fig. 11F). On most specimens, the inner shell layers consists of a mosaic of clear calcite, but on some specimens (including the type specimen of *M. ramanensis*) the inner shell contains layers of irregular stubby calcite prisms, 2–3 mm long and 1–1.5 mm wide (Text-fig. 11A–C). These thick inner shell sublayers may have been secreted as original calcite. A subdued lamellose condition (Text-fig. 5), formed by the thin outer shell layer, is present on the apical portions of well-preserved valves, changing to more extended, irregular lamellae on the posterior part of mature individuals.

Types and figured specimens. Holotype is NRM-PZ Mo152775 (Naturhistoriska Riksmuseet – The Swedish Museum of Natural History); specimens figured in this study are reposited in the same collection and numbered NRM-Mo161125-161137.

Occurrence. Known only from the Gevanim Formation, Negev Desert, Israel, Late Anisian.

Discussion. Brotzen (1956, p. 209) described *Myalina ramanensis* as having a 'shell equivalvated (*sic*), obliquely elongated, hinge margin long and straight, apical angle about 45, length:breadth about 5:3, length:height of each valve 5:2, average length 15 cm. Characterized by a sharp,

S-shaped crest near the posterior margin. Surface more or less smooth, with concentric undulations'. The type specimen of *R. ramanensis* is a well-formed individual with rounded lateral margins and no irregularities except for a broken posterior margin and loss of the posterior portion of the crest. This specimen is wider than other specimens available for study but appears to be a typical example of the species.

The basal surface of most mature individuals has a broad curvature that bows anteroventrally (functionally

ventral), with maximum inflation at mid-valve (Text-figs 4, 7). Some individuals have a more flattened basal surface, but these are the result of either growth irregularity or post-burial deformation, and none has a truly flat basal surface. This 'rocking chair' profile is the result of adaptation to edgewise reclining life habit by moderate size bivalves. It is not developed on larger edgewise recliners, which have flatter basal surfaces.

Mature shells acquire a thick infilling of secondary shell that covers the inner surface of the umbos, hinge and anterior portion of the basal surface, fusing the valves together and preventing further opening or closing of the valves (Text-fig. 7). This results in hinge obsolescence and a nonfunctional hinge for the adult. On the apical half of the basal surface, the valves thicken and are tightly appressed against each other, although not completely fused with secondary internal secretions. Opening to the outside is maintained on the posterior margin. When valves fuse, growth along the posteroventral portion of the basal surface continues by adding to valve margins, resulting in an overlapping of valve edges and a doubled shell in that area (Text-fig. 8B). The development of growth overlap is variable and either valve may be on the exterior. In the specimens examined, five have the left valve exterior, and three have the right valve exterior in the zone of overlap. Shell disarticulation may occur before fusion begins, usually resulting in slippage and permanent displacement of the valves (Text-figs 4A, D, 10). This produces an apparent discordance in valve size. Slippage may occur in any direction, and either valve may be smaller as a result of inhibited growth. One specimen examined has valves pushed apart (Text-fig. 10) and the area of separation filled with secondary shell material that fused the valves together. Because of this irregular growth condition, the mature form of shells is variable. The common misalignment of valves is not a preservational accident, but is present in most specimens and is preserved by later infilling of the beaks with secondary shell layers.

Valve fusion, overlapping of valve margins, valve displacement at maturity and development of an irregularly lamellose posterior margin that is probably flexible are the most unusual features of this genus. These characters are interrelated and develop as a consequence of the weak ligament that is incapable of holding heavy, thick-shelled valves in position. Ligament failure is considered to be the reason for valve slippage (Text-fig. 4A, D) and valve separation (Text-fig. 10) at the adult growth stage, stimulating the bivalve to secrete more shell in the beak area and ultimately producing fusion of the valves. Subsequent growth is limited to abapical portions of the shell, where a thin irregular shell margin develops on the posterior margin. This is the only margin with effective access to ocean waters and is thin and usually curved, described by Brotzen (1956) as an S-shaped crest. This feature is irregularly developed, with either a left-hand deflection or a right-hand deflection, but it is not present on all individuals in a population. On some specimens, the crest irregularity is produced or exaggerated by post-depositional sediment compaction. This inconstancy of development indicates that the feature is not strongly controlled and develops because of the thinness of shell on that margin, either as a biological response that allows the animal to maintain an opening to the water column or because of post-burial deformation of the thinner shell margin by sediment compaction. Even when present, the S-shaped crest of *Ramonalina ramanensis* cannot be considered a species-specific character. The posterior shell margin remained thin and produced irregular extended lamellae separated by open spaces, perhaps occupied by conchiolin sheets during life. A conchiolin-thickened shell margin would have some flexibility, and this type of shell margin would be compatible with fusion of valves on adults; serving to maintain a water connection to the interior.

Brotzen (1956) indicates that several species are present in the Makhtesh Ramon section. The two that he described are here placed in *Ramonalina*, but other species remain undescribed. Because of the variability of *R. ramanensis* described here, the other shell morphologies may be contained in the range of variation of the two described *Ramonalina* species, but that remains to be determined with larger samples. The older species *R. beneckei* (Brotzen 1956) is smaller, with more prominent beaks and less flattened on the basal surface, but the juvenile byssal notch and occurrence of valve displacement is similar (Brotzen 1956).

MOUND BUILDING BY RAMONALINID BIVALVES

The *Ramonalina*-dominated mounds in the Gevanim Formation are the largest Middle Triassic bivalve mounds known. The mounds are as much as 7 m thick and of wide lateral extent (Text-fig. 2) and form a stratigraphic unit exposed over a distance of 2.5 km. Other occurrences of Middle Triassic bivalve mounds are limited to small (metre-scale) constructional mounds made by the small cementing bivalve *Placunopsis* in the Muschelkalk of central Europe (Flügel and Senowbari-Daryan 2001; Bachmann 1979, 2002). Bivalves are not a normal component of Anisian mounds and reefs built by taxa of the coral-sponge-*Tubiphytes* association (Flügel and Senowbari-Daryan 2001; Payne *et al.* 2006). *Ramonalina*-dominated mounds are more like the *Promyalina*-dominated myalinid shell beds (Birkenmajer 1977; Krystyn *et al.* 2003) of the Early Triassic and the shell beds produced by megalodontids during the Late Triassic. All of these lack attached framework taxa.
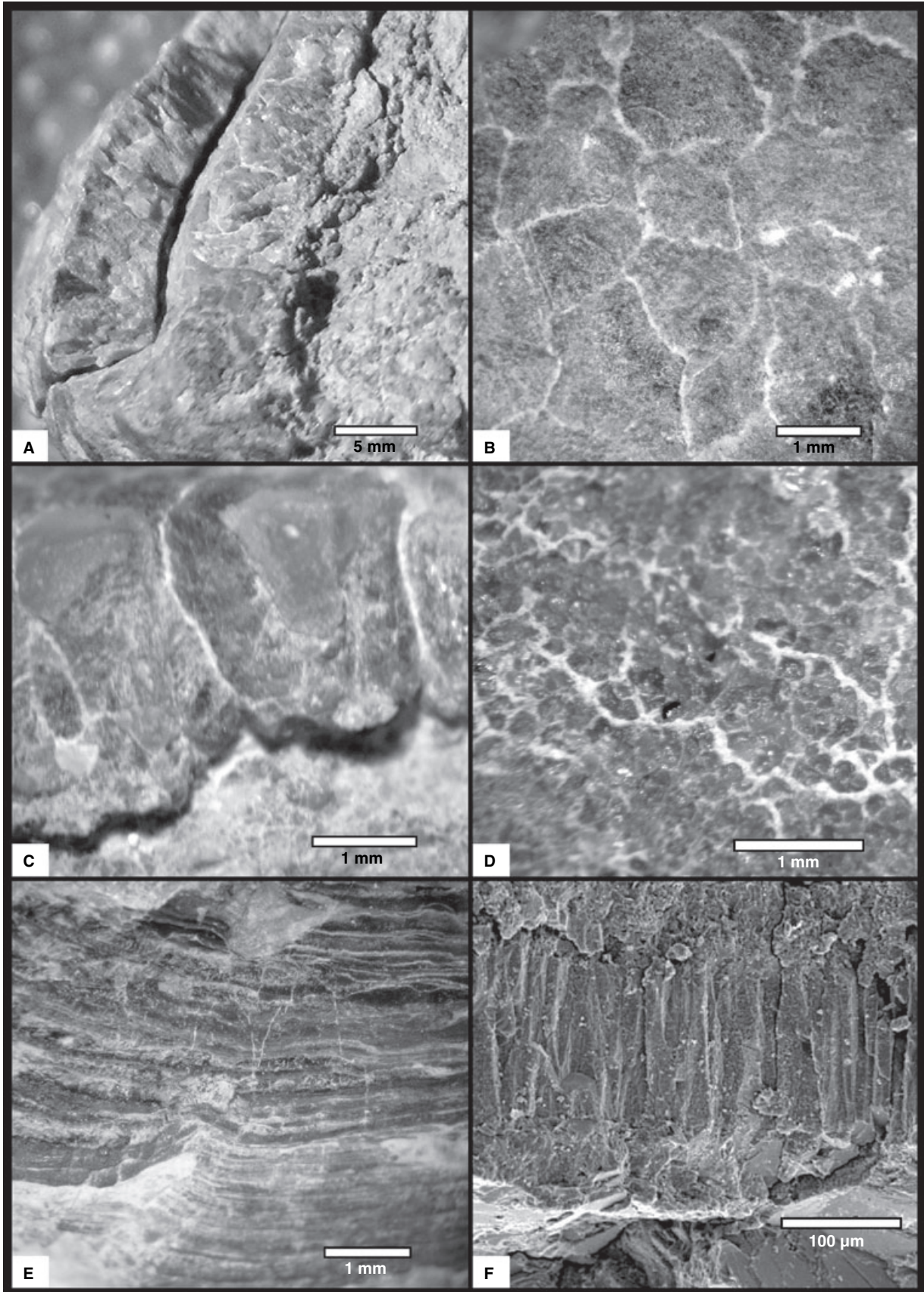
Ramonalina-dominated mounds are most similar to Carboniferous shell beds of myalinids, the dominant shell bed producers in marginal marine settings of the Late Palaeozoic. Ramonalinids and myalinids both form tabular shell layers, lenses or mounds consisting mostly of adult-sized shells of one species. These assemblages may contain a few other macrofossils and often contain some encrusting organisms (such as microconchids) and/or boring taxa (especially the slit-shaped barnacle boring *Rogerella*), but in many instances accompanying taxa are rare or may be absent except for encrusters. This type of accumulation, characterized by low biotic diversity and dominated by a species with a large and thick shell, is well described by Lobza *et al.* (1994) and West *et al.* (1996).

The Makhtesh Ramon mounds have a matrix of mixed carbonate–siliciclastic mud, with minimal cement. The presence of mixed carbonate–siliciclastic mud matrix and laterally extensive mud layers (see top layers of 'Myalina Reef' in Text-fig. 2) within the Makhtesh Ramon deposit point to a mud-adapted life preference for *Ramonalina*.

It appears that the shape of the shells, each with a crest rising above the sediment surface, provided a baffling structure for mud accumulation among the bivalves and promoted the continued buildup of the mound. The fabric of the ramonalinid mounds is similar to the fabric of other Anisian mounds and reefs, consisting of a matrix composed mostly of carbonate mud with little cement. Despite the presence of basally attached corals and sponges capable of producing a cemented framework, these skeleton producers in the coral-sponge-*Tubiphytes* Anisian reefs acted primarily as bafflers in reef construction (Flügel and Senowbari-Daryan 2001).

Lerman (1960) and Druckman (1974) considered the Unit 40 mounds to have been similar to modern mytilid banks in tidal channels, but the great lateral extent of the unit implies a placement on shallow subtidal mud flats, perhaps in areas subject to some variation in water salinity, turbidity and energy level. It is reasonable to infer that the Makhtesh Ramon deposit occurred in shallow or marginal marine environments similar to that favored by myalinids, where variations in salinity protected the bivalves from strong predation from stenohaline organisms. The abundance of vertebrate teeth and bone suggests an abundance of food in the environment.

Ramonalina-dominated mounds are unusual, because they are formed by free-living edgewise reclining bivalves. Edgewise recliners are adapted to life on a mud substrate and tend to grow to large size, a life habit that tends to preclude continuous accumulation to form upwards-growing mounds. The mound-building ability of *Ramonalina* is associated with the moderate growth size (15 cm) of adult shells, allowing closer packing of shells and a longer proportion of the life cycle spent as a byssally attached juvenile. However, adult growth required resting on a mud substrate to achieve proper positioning.

ADAPTIVE MORPHOLOGY AND EDGEWISE RECLINING LIFE HABITS

Ramonalina acquired a flattening that is an adaptation to resting on the surface of a substrate (snowshoe support). The general form is not much different from two other groups of edgewise recliners: Middle Permian alatoconchids (ambonychioids) and Late Triassic wallowaconchids (megalodontoids). All three groups have a flattened basal surface formed by folding both valves into wing-like structures, an ovoid substrate parallel shape with broad rounded sides and a high crest produced by the posterodorsal end of the hingeline. This shell shape develops as a consequence of adapting to an edgewise reclining life habit. A flat ovoid basal surface is the most effective design for maintaining position, and there is homeomorphic convergence to this shape. Early Jurassic *Opisoma* (astartids) also develops a generally similar shape, but it is less specialized and lacks a prominent crest (Aberhan and von Hillebrandt 1999).

Although intermediate in age between alatoconchids and wallowaconchids, the ramonalinids are only distantly related to either group. The similarity of general form among alatoform edgewise recliners – flattened basal surface, pointed beak and elevated crest in an posterodorsal position – and occurrences with great numbers of individuals in monospecific accumulations shows the value of this life habit in shallow mud-bottomed environments during the Permian and early Mesozoic. The short duration of these occurrences suggests alatoform bivalves appeared as an opportunistic response to the availability of large amounts of food, but were either adapted to a

TEXT-FIG. 11. Shell microstructure of *R. ramanensis* (Brotzen, 1956). A, cross-section view of two layers of large prisms on abapical margin of left wing. B, exterior end view of coarse prisms on dorsal part of valve. C, side view of coarse prisms on dorsal part of valve. D, exterior end view of small prisms in simple columnar prismatic layer; this is the typical size of prisms in shell layers. E, crowded growth lines and small lamellae formed by dark outermost shell layer, located in recess formed by valve margins on basal surface of shell. Holotype specimen of *R. ramanensis* (Brotzen, 1956), NRM-PZ Mo152775. F, dark outermost shell layer composed of calcite prisms oriented perpendicular to surface. Large crystals at base of photo are mosaic calcite of inner shell layer; small crystals above prism layer are part of the matrix. Specimen NRM-PZ Mo161131.

narrow range of environmental conditions or were susceptible to predation.

Ramonalina and other edgewise recliners utilizing snowshoe support had adaptations that contrast with the varied adaptations of other recliners (Seilacher 1984). Edgewise recliners produced large heavy shells, effectively precluding low density floating in a denser medium (iceberg-style positioning). The implications of this growth habit are that edgewise recliners utilized firm mud substrates, associated with moderate rates of mud accumulation and lower intensity of biogenic reworking of the oxic mud layer. Edgewise reclining is one of several morphological adaptations (edgewise reclining, cup reclining, fan reclining, bent tube reclining, mud sticking) that allow bivalves to position at the mud sediment surface.

The secretion of large amounts of shell carbonate and ability to produce very large numbers of individuals in small areas prompts the question: did ramonalinids carry microalgal symbionts? The appearance of obligate dinoflagellate-bearing hermatypic corals in the middle Triassic (see Flügel 2002) indicates that this type of association is possible for other metazoans, including the ramonalinids. Microalgal symbiosis is present in some heavy carbonate-secreting groups, including large benthic foraminiferans, hermatypic corals and tridacnid bivalves, and it is common in cardiid bivalves (Ohno *et al.* 1995; Lee 2006; Schneider 1996). The first three groups are obligate symbionts of microalgae (primarily the dinoflagellate *Symbiodinium*) and flourish in shallow marine waters characterized by carbonate sediment deposition (Wood 1996). This differs with the inferred environment for *Ramonalina*, which lived on mixed carbonate-siliciclastic sediment in waters that probably had high nutrient levels. However, symbiosis with microalgal or other microbial symbionts is common among bivalves and a surface-dwelling edgewise recliner and heavy carbonate shell-secreting organism like *Ramonalina* is likely to have housed microalgal symbionts in its tissue. Because the environment is inferred to have had high nutrient levels, if *Ramonalina* housed microalgae in its tissue, the relationship was probably non-obligate and variable in degree of development.

CONCLUSIONS

The newly described genus *Ramonalina* is an edgewise-reclining large bivalve found in nearly monospecific mounds of the early Middle Triassic (Late Anisian) of southern Israel (Gevanim Formation). It is descended from myalinids and is here defined as the type genus of a new bivalve family, the Ramonalinidae, characterized by thick shells with a duplivincular ligament of numerous very narrow nearly horizontal ligament grooves and strongly folded valves that formed a nearly flattened basal surface for edgewise reclining.

Mature specimens of *Ramonalina ramanensis* (= *Myalina ramanensis* Brotzen, 1956) are characterized by a thick secondary shell on much of the inner valve surfaces, which fused the valves together and rendered the hinge nonfunctional. Some shells disarticulated before fusion, resulting in permanently misaligned valves and discordant valve sizes. Shell growth in mature and fused specimens of *R. ramanensis* continued along the posterodorsal margin producing a thin, possibly conchiolin-reinforced shell margin that would have had to have some flexibility to maintain a connection between the valve interior and the water.

Ramonalinid mounds developed on a muddy substrate in a shallow marginal marine environment, and shells in the mounds are embedded in a matrix of carbonate-siliciclastic mud. The functionally dorsal crest probably acted to baffle sediment and promote mud accumulation in the mound. The thick carbonate shell of the ramonalinids and fused shell condition as adults, their living environment, and comparison to modern bivalve analogues, suggests that their mantle tissues housed microalgal symbionts, but only as a non-obligate condition.

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