

Middle Jurassic (Callovian) cyclostome bryozoans from the Tethyan tropics (Matmor Formation, southern Israel)

MARK A. WILSON, STEPHANIE BOSCH & PAUL D. TAYLOR



A tropical Jurassic bryozoan fauna is described here for the first time. The Matmor Formation (Callovian, upper *Peltoceras athleta* Zone) contains six cyclostome bryozoan species in five genera. Four of these species are new: *Microeciella yoavi*, *Idmonea snehi*, *Hyporosopora nana*, and *Hyporosopora negevensis*. The Matmor Formation was deposited on a shallow shelf near the palaeoequator on the southwestern margin of the Tethys Ocean, within the Ethiopian Province of the Tethyan Faunal Realm. The Matmor bryozoans share genera with contemporary, non-tropical faunas in Europe, having the most similarities with Callovian assemblages in Poland. The low species richness of the Matmor bryozoan fauna is not unusual for the Jurassic but they do appear to be less abundant than contemporaneous fully marine bryozoan faunas from higher palaeolatitudes. The unusually small zooids of the Matmor bryozoans may be a function of the temperature-size rule because this fauna developed in shallow, warm, tropical waters. • Key words: Bryozoa, Cyclostomata, Callovian, Jurassic, Israel.

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The Middle Jurassic was a time of diversification and innovation in the Phylum Bryozoa, especially among the cyclostomes (Taylor & Ernst 2008). Most of the data on Jurassic bryozoan faunas comes from Europe (see, for examples, Walter 1970; Hara & Taylor 1996, 2009; Taylor 2009; Viskova 2006, 2007, 2008, 2009; Zatoń & Taylor 2009, 2010; Zatoń *et al.* 2013) with a few North American occurrences (see Cuffey & Ehleiter 1984, Taylor & Wilson 1999), which were situated at palaeolatitudes to the north of the Jurassic tropics. Sclerobionts (hard substrate dwellers; Taylor & Wilson 2002) in general commenced a significant diversification in the Callovian and began to resemble their modern counterparts (Zatoń & Vinn 2011). This was also a time when marine communities were consolidating following the first pulse of the Mesozoic Marine Revolution (Vermeij 1977, 2008; Aberhan *et al.* 2006). A bryozoan fauna from the tropics of the Jurassic is described here for the first time, adding to the single species described by Newton (1921) from the ?Upper Jurassic of Bachain, near Riyadh, Saudi Arabia. This provides new information about latitudinal bryozoan diversity gradients in the Jurassic, and contributes to a global perspective on Jurassic marine community evolution.

Only recently have geologists begun to systematically describe and interpret the palaeoecological and palaeogeographical contexts of Jurassic tropical marine faunas. Thus far, most of the investigated fossils have been from shallow Tethyan shelf deposits in the Middle East (*e.g.*, Feldman & Brett 1998; Pandey *et al.* 2000; Wilson *et al.* 2008, 2010; Ausich & Wilson 2012; Feldman *et al.* 2012). The fossils in this region are well exposed and quite well preserved, and they can be collected in a well-defined lithostratigraphic and biostratigraphic framework.

Geological setting

All the bryozoans in this study come from a single unit of fossiliferous marl in the Matmor Formation (Callovian) exposed in the Matmor Hills of Hamakhtesh Hagadol (an erosional basin similar to a breached anticline; Avni 2001) in southern Israel. The Matmor Formation is approximately 120 metres of lagoonal and reefal marls and limestones lying conformably above the Zohar Formation (also Callovian) and disconformably below the Lower Cretaceous



Figure 1. Location of field site Hamakhtesh Hagadol in southern Israel. See Table 1 for specific localities within the makhtesh.

(Aptian) Hatira Formation (Hirsch & Roded 1997). Originally considered as upper Callovian and lower Oxfordian (e.g., Hudson 1958), ammonites (Gill *et al.* 1985, Cariou *et al.* 1997, Hirsch *et al.* 1998) and foraminifera (Grossowicz *et al.* 2000) now show that the entire Matmor Formation is Callovian. The lower 30 metres of the Matmor (subunits 43–52; Goldberg 1963) belong to the *Peltoceras athleta* Zone, and the subunits above are in the *Quenstedtoceras (Lamberticeras) lamberti* Zone of the Upper Callovian (Hirsch *et al.* 1998).

The Matmor Formation was deposited near the palaeoequator during late Callovian times on the southern margin of the Tethys (Golonka 2004). This was within the Ethiopian Province of the Tethyan Faunal Realm (Feldman *et al.* 2001). The horizon from which the bryozoans described here were collected (subunit 51; Goldberg 1963) was part of the J40 major maximum flooding event across the Arabian Platform at approximately 163 Ma (Sharland *et al.* 2004), which was a result of an apparent global rise in sea level (Wierzbowski *et al.* 2009). This transgression facilitated the development of numerous calcareous sponge and coral patch reefs with lagoonal marls throughout the region (Haq & Al-Qhatani 2005).

The bryozoans in the Matmor Formation are accompanied by a rich shallow marine fauna of sponges (Wood

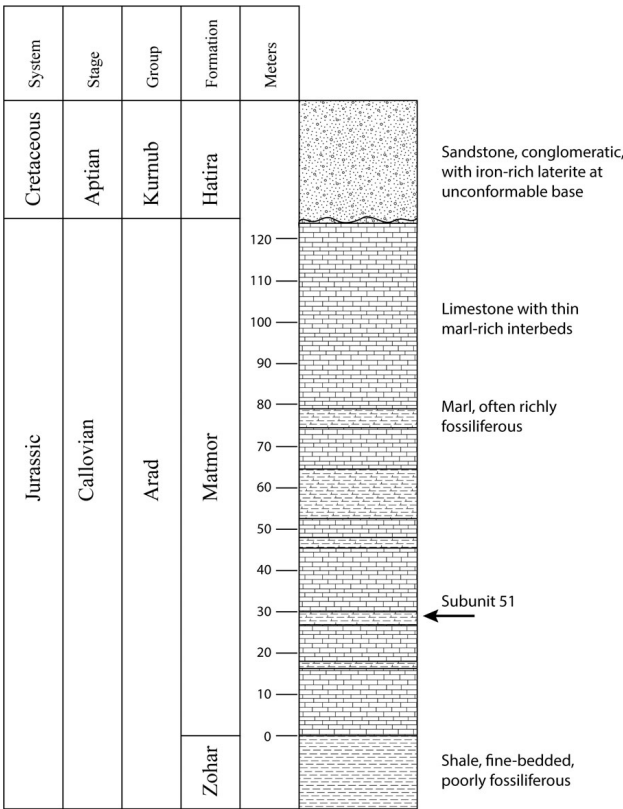


Figure 2. Stratigraphic column of the Matmor Formation exposed within Hamakhtesh Hagadol (Fig. 1). All the bryozoans described in this study were collected from Subunit 51 of Goldberg (1963).

Table 1. Locations of the bryozoans collected for this study at Hamakhtesh Hagadol, southern Israel (Fig. 1). All are in subunit 51 (Goldberg 1963) of the Matmor Formation, which is 25–30 metres above the base.

Location #	Coordinates
C/W-172	N 30.93369°, E 34.97588°
C/W-173	N 30.92907°, E 34.97295°
C/W-247	N 30.95040°, E 35.00758°
C/W-366	N 30.94919°, E 35.01109°
C/W-371	N 30.94220°, E 34.98131°
C/W-600	N 30.93837°, E 34.979069°
C/W-602	N 30.93549°, E 34.97683°
C/W-608	N 30.94916°, E 35.01110°
C/W-609	N 30.929081°, E 34.972984°

1987, 1999), corals (Wilson *et al.* 2010), brachiopods (Feldman *et al.* 2001), bivalves (Hirsch 1979), gastropods (Reiner 1968), ammonites (Gill & Tinant 1975, Gill *et al.* 1985, Lewy 1983) and crinoids (Ausich & Wilson 2012). The sclerobionts (hard substrate dwellers; Taylor & Wilson 2003) have lately been described in some detail. They include serpulid and sabellid tubes (Vinn & Wilson 2010), thecideide brachiopods (Krawczyński & Wilson 2011), and a variety of borings (Wilson *et al.* 2008, 2010).

Almost all the bryozoans described in this paper encrust pluricolumnals and holdfasts of the large articulate crinoid *Apiocrinites negevensis* Ausich & Wilson, 2012. A few are found on pluricolumnals of a smaller crinoid, *Apiocrinites feldmani* Wilson et al., 2014. The bryozoans appear to be *post mortem* encrusters on the crinoids because they often extend over articulating surfaces.

Localities, methods and materials

The bryozoans described here are from subunit 51 (Goldberg 1963) of the Matmor Formation (Middle Jurassic, Callovian, upper *Peltoceras athleta* Zone) exposed in the Matmor Hills of Hamakhtesh Hagadol, southern Israel (Fig. 1). Subunit 51 is 28–30 metres above the base of the formation (Fig. 2). Table 1 lists the specific localities with location numbers and coordinates.

Approximately 130 bryozoan colonies were found encrusting primarily crinoids (*Apiocrinites negevensis* and *A. feldmani*), with a few on echinoids, bivalves and ammonites. These were cleaned in an ultrasonic bath and examined with a binocular microscope. Well-preserved specimens were measured with a Nikon SMZ1500 video-microscope and CellSens Standard imaging software. The most representative and diagnostic specimens were further studied and imaged using a LEO 1455VP low vacuum scanning electron microscope housed at the Natural History Museum, London.

Following the definitions of Zatoń et al. (2013, p. 838), we use the term “gonozooid” for the entire fertile zooid and “brood chamber” for the distal, expanded portion of the gonozooid in which the embryos would have been housed.

Type and figured specimens are deposited in the fossil collections of the Natural History Museum, London (NHMUK).

Systematic palaeontology

Order Cyclostomata Busk, 1852

Family Stomatoporidae Pergens & Meunier, 1886

Genus *Stomatopora* Bronn, 1825

Type species. – *Alecto dichotoma* Lamouroux, 1821, by monotypy; Bathonian of Calvados, France.

Stomatopora aff. *dichotomoides* (d’Orbigny, 1850)

Figure 3A–D

Material. – Numerous colonies encrusting biogenic debris, especially ossicles of the crinoid *Apiocrinites* (NHMUK BZ 7720, 7721, 7723).

Measurements. – Autozooid width (proximal) 0.06–0.22 mm (mean = 0.12 mm; n = 68); autozooid width (distal) 0.11–0.37 mm (mean = 0.18 mm; n = 68); autozooid length 0.31–0.64 mm (mean = 0.47 mm; n = 40); longitudinal aperture diameter 0.04–0.10 mm (mean = 0.06 mm; n = 18); transverse apertural diameter 0.03–0.07 mm (mean = 0.05 mm; n = 18).

Description. – Encrusting, uniserial colonies with bifurcation every other autozooid (Fig. 3A–C). Bifurcation angles initially range from 130° (Fig. 3A) to 180° (Fig. 3B, C); subsequent angles are less than 90°. No complete ancestrula was found; the best-preserved example is broken and was at least 0.10 mm long (Fig. 3C). Autozooids with irregular shape depending on substrate; most slightly expand in width distally. Peristomes not preserved except for an occasional base (Fig. 3D). Pseudopores on the autozooids are circular and with somewhat irregular spacing.

Discussion. – This is the most common bryozoan in the Matmor fauna, yet we leave it in open nomenclature. Hara & Taylor (1996, 2009) emphasized the value of zooid frontal wall widths in taxonomic assessment, and this technique is especially useful with species of *Stomatopora*. The Matmor *Stomatopora* species is significantly smaller than the other described species in zooid length, but the range of zooid distal width falls within the measurements of *S. cf. dichotomoides* described by Zatoń et al. (2013). Without a complete ancestrula, and early astogeny, we cannot definitively place the Matmor specimens in this species. For a partial synonymy of *S. dichotomoides*, see Hara & Taylor (2009).

Occurrence. – C/W-172, C/W-173, C/W-247, C/W-366, C/W-600, C/W-602, C/W-608, C/W-609 (Table 1).

Family Oncousoeciidae Canu, 1918

Genus *Oncousoecia* Canu, 1918

Type species. – *Tubulipora lobulata* Canu, 1918; Recent, British Isles; see Taylor & Zatoń (2008).

Oncousoecia sp.

Figure 4A–D

Material. – Three colonies encrusting a pluricolumnal of *Apiocrinites negevensis* (NHMUK BZ 7723, NHMUK BZ 7724).

Measurements. – Autozooid frontal wall width 0.08 to 0.13 mm (mean = 0.10 mm; n = 23); frontal wall length 0.28–0.31 mm (mean = 0.29 mm; n = 5); longitudinal aperture diameter 0.05–0.10 mm (mean = 0.07 mm; n = 21);

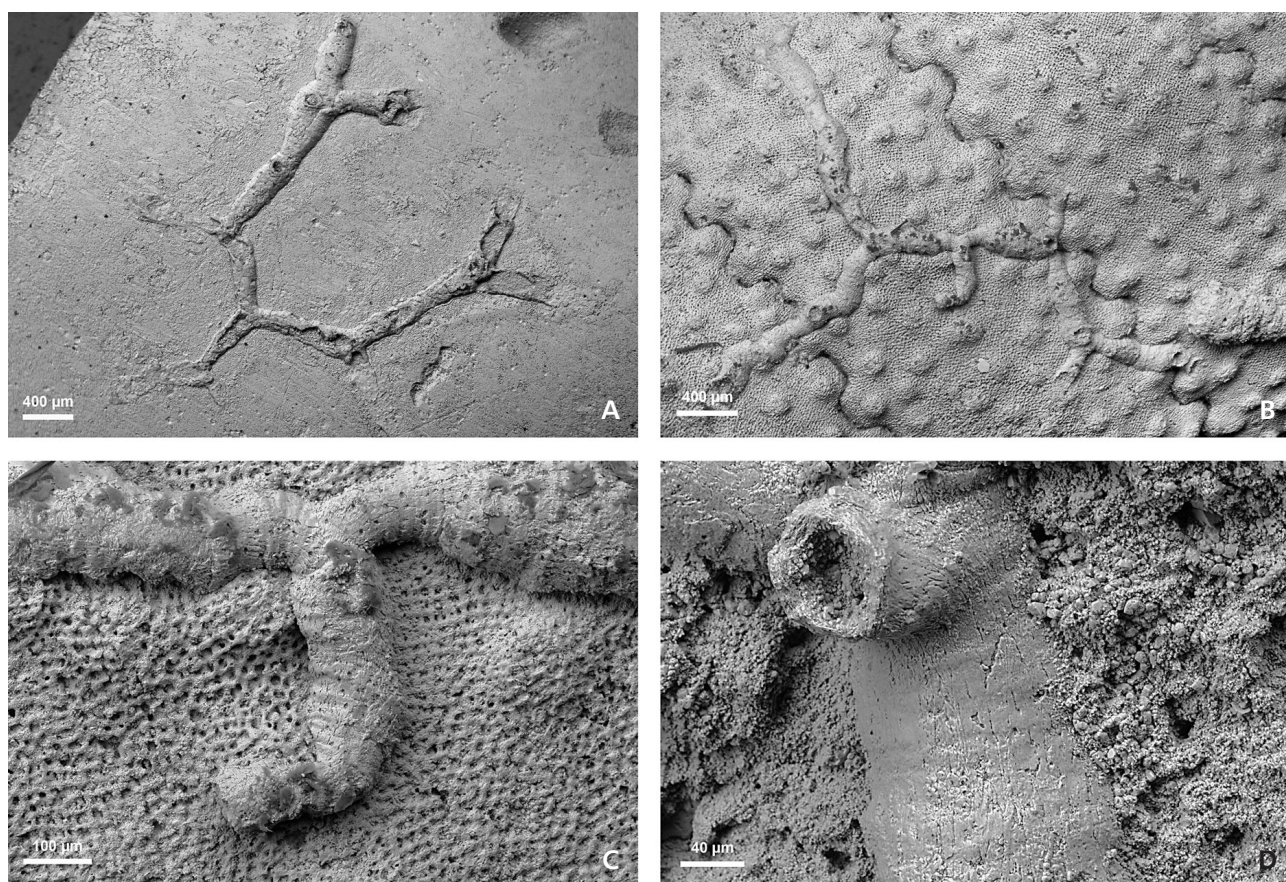


Figure 3. *Stomatopora* aff. *dichotomoides* (d'Orbigny, 1850) encrusting crinoid ossicles from the Matmor Formation (Callovian) of Hamakhtesh Hagadol, southern Israel. • A – partial colony showing abraded early zooids and initial branching angle, NHMUK BZ 7720; B – early portion of colony showing broken ancestrula, NHMUK BZ 7721; C – closer view of B with broken ancestrula and early autozooids; D – single autozoid with partial peristome, NHMUK BZ 7722.

transverse aperture diameter 0.04–0.07 (mean = 0.05 mm; $n = 21$). Proximal portion of corroded gonozooid is approximately 0.30 mm long; ovoidal brood chamber is approximately 0.40 mm wide and 0.20 mm long.

Description. – Known from three eroded colonies in the Matmor Formation (Fig. 4A–C). Colonies encrusting, multiserial, expanding from one autozooid wide to at least 14. Autozooids elongate, with circular pseudopores. One corroded gonozooid has a long, narrow proximal portion and a small, transversely ovoidal brood chamber (Fig. 4D). Another corroded gonozooid has a broken and unroofed brooding chamber.

Discussion. – With only three colonies found, this is the least common bryozoan species in the Matmor Formation. We have left it in open nomenclature because the gonozooids are too eroded for full characterization. Nevertheless, we can say that the Matmor *Oncousoecia* is not the same as *Oncousoecia* sp. 1 of Zatoń *et al.* (2013) from the Middle Jurassic of Poland because its frontal wall widths are signifi-

cantly smaller (0.10 vs 0.30 mm). *Oncousoecia* sp. 2 of Zatoń *et al.* (2013, p. 842) also has wider frontal walls and a “longitudinally ovate” gonozooid contrasting with the transversely ovoidal gonozooid of the Matmor *Oncousoecia*. The Middle Jurassic *Oncousoecia* from Balin, Poland, described by Taylor (2009) has considerably larger autozooids (0.33–0.40 mm wide) and longitudinally elliptical pseudopores compared to the circular pseudopores of this species. Gonozooids are unknown in ?*Oncousoecia* sp. 1 and ?*O.* sp. 2 of Taylor & Wilson (1999) from the Middle Jurassic of Utah, USA, but the autozooid frontal wall widths (0.75 to 1.38 mm and 0.19–0.26 mm, respectively) in these species are significantly larger than the Matmor specimens.

Occurrence. – C/W-608 (Table 1).

Genus *Microeciella* Taylor & Sequeiros, 1982

Type species. – *Microeciella beliensis* Taylor & Sequeiros, 1982; Jurassic (Toarcian) of Belchite, Spain.

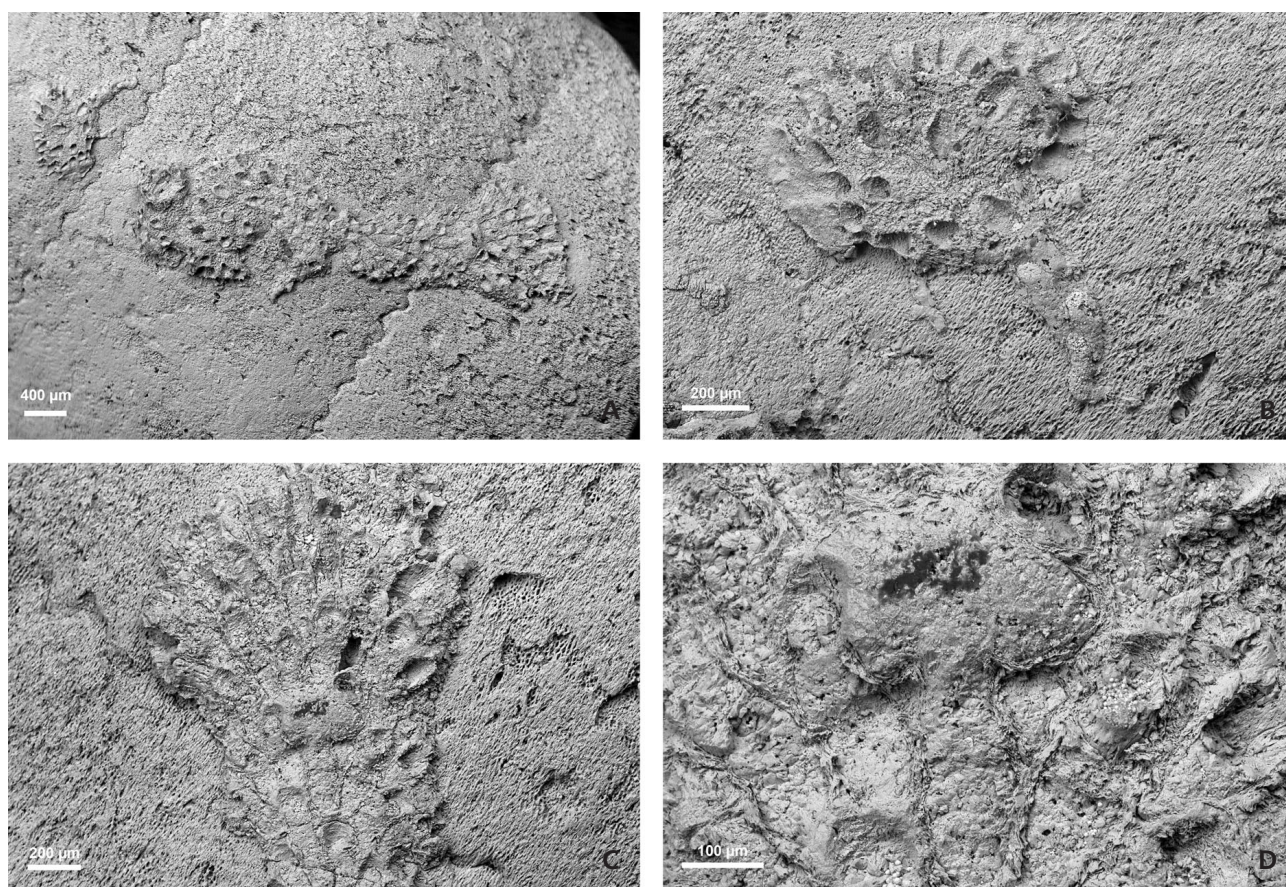


Figure 4. *Oncousoecia* sp. encrusting a crinoid pluricolumnal from the Matmor Formation (Callovian) of Hamakhtesh Hagadol, southern Israel, NHM UK BZ 7723. • A – two colonies; B – smaller of the colonies in Fig. 4A with abraded ancestrula; C – larger of the colonies in Fig. 4A; D – corroded gonozooid of the larger of the colonies in Fig. 4A.

***Microeciella yoavi* sp. nov.**

Figure 5A,B

Types. – Holotype: NHMUK BZ 7725 (Fig. 5A, B).

Type locality. – C/W-602; Matmor Formation (Middle Jurassic, Callovian, upper *Peltoceras athleta* Zone) in the Matmor Hills near the centre of Hamakhtesh Hagadol in southern Israel (Table 1).

Type horizon. – Subunit 51 (see Goldberg 1963) of the Matmor Formation, approximately 28 metres above the base of the unit.

Etymology. – Species named for Yoav Avni, a geologist with the Geological Survey of Israel who has organized palaeontological fieldwork in southern Israel and assisted with discovery and collection.

Material. – One colony with a gonozooid imaged and measured (NHMUK BZ 7725); numerous eroded colonies in collection.

Measurements. – Autozooid frontal wall width 0.07 to 0.10 mm (mean = 0.08 mm; $n = 12$); frontal wall length 0.24 to 0.27 mm (mean = 0.26 mm; $n = 5$); longitudinal aperture diameter 0.04–0.05 mm (mean = 0.05 mm; $n = 6$); transverse aperture diameter 0.03–0.05 (mean = 0.04 mm; $n = 6$). Holotype gonozooid proximal portion 0.27 mm long, 0.09 mm wide; distal brood chamber 0.30 mm long, 0.38 mm wide; total gonozooid length 0.58 mm; oöciopore diameter 0.05 mm.

Description. – Colony encrusting, sheet-like, discoidal (Fig. 5C), multiserial, unilamellar. Autozooids small, elongate with convex frontal walls crossed by prominent growth bands; apertures small, circular to ovoidal; peristomes either short or abraded away (Fig. 5C); pseudopores subcircular and regularly spaced (Fig. 5D). Gonozooid distinctive, with a long proximal portion and a spherical brood chamber (Fig. 5C); dense array of circular pseudopores on brood chamber; oöciopore terminal and about the same diameter as the autozooid apertures, strongly transversely elongate.

Discussion. – *Microeciella yoavi* sp. nov. may be relatively

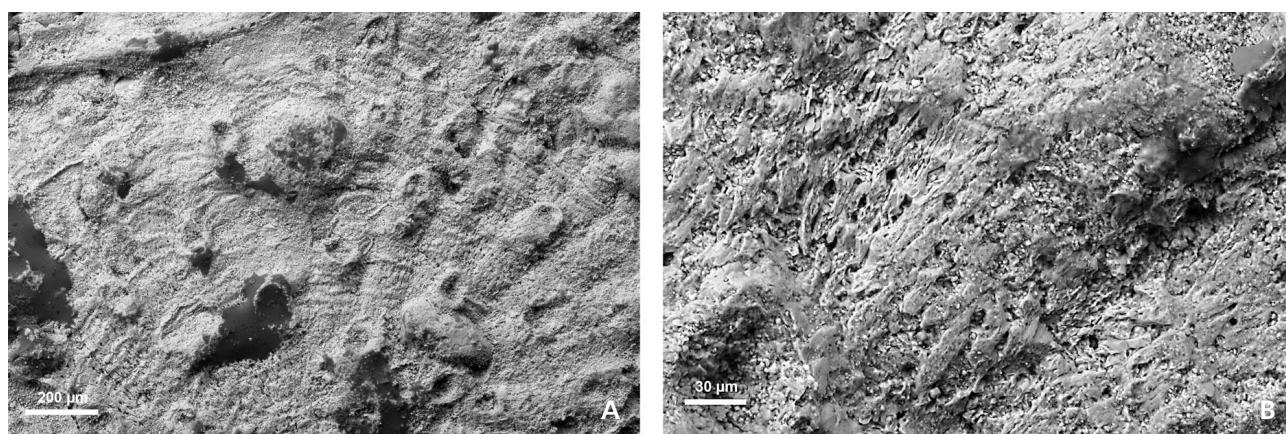


Figure 5. *Microeciella yoavi* sp. nov. encrusting crinoid ossicles from the Matmor Formation (Callovian) of Hamakhtesh Hagadol, southern Israel. • A – part of a circular colony with complete gonozooid, NHMUK BZ 7725 (a); B – closer view of colony in Fig. 5A showing pseudopores on autozoid frontal walls, NHMUK BZ 7725 (a).

common in the Matmor bryozoan fauna, but we have only one with a preserved gonozooid that enables secure identification. This species resembles *M. cf. matisconensis* and *M. calloviana* described in Zatoń *et al.* (2013) from the Middle Jurassic of Poland. *M. yoavi* sp. nov., however, has significantly smaller autozooids (frontal wall width 0.07–0.12 mm compared to 0.10–0.17 and 0.14–0.16 mm, respectively) and a tiny, more spherical brood chamber.

Occurrence. – C/W-602 and C/W-608 (Table 1).

Family Multisparidae Bassler, 1935

Genus *Idmonea* Lamouroux, 1821

Type species. – *Idmonea triquetra* Lamouroux, 1821; Bathonian of Calvados, France.

Idmonea snehi sp. nov.

Figure 6A–D

Types. – Holotype: NHMUK BZ 7726 (Fig. 5A–D); paratype: NHMUK BZ 7725(b).

Type locality. – C/W-247; Matmor Formation (Middle Jurassic, Callovian, upper *Peltoceras athleta* Zone) in the Matmor Hills near the centre of Hamakhtesh Hagadol in southern Israel. (See Table 1 for localities in subunit 51 of Goldberg 1963.)

Type horizon. – Subunit 51 (see Goldberg 1963) of the Matmor Formation, approximately 25 metres above the base of the unit.

Etymology. – Species named for Amihai Sneh, a geologist

with the Geological Survey of Israel who first encouraged this work.

Material. – Two colonies (NHMUK BZ 7726, 7725(b)).

Measurements. – All measurements from holotype. Width of branches 0.21–0.63 mm (mean = 0.42 mm; $n = 10$); lateral budding angle of branches 76° – 124° (mean = 97° ; $n = 4$). Autozoid frontal wall width 0.07–0.17 mm (mean = 0.11 mm; $n = 30$); frontal wall length 0.22 to 0.33 mm (mean = 0.26 mm; $n = 21$); longitudinal aperture diameter 0.03–0.10 mm (mean = 0.07 mm; $n = 25$); transverse aperture diameter 0.03–0.09 mm (mean = 0.06 mm; $n = 26$).

Description. – Colony encrusting, with ribbon-like branches up to five autozooids wide, low and rounded in profile (Fig. 6A–C); lateral branches bud haphazardly at 76° – 124° from the flanks of a parent branch, emerging from the aperture of an autozoid (Fig. 6A); terminal branch bifurcation not observed. Autozooids elongate but with indistinct zooidal boundaries; apertures circular or slightly transversely elongate, some with terminal diaphragms; peristomes either short or abraded (Fig. 6A–C). Kenozooids form a wide selvedge along the branch margins, distally diverging from the axis and tapering in height (Fig. 6B). Pseudopores circular, dense and well preserved across the autozoid frontal walls; less dense on kenozooids. Gonozooids not observed.

Discussion. – Mean autozoid size from the Matmor specimens fits well within the size range of the *Idmonea* sp. described from the Maastrichtian (Upper Cretaceous) by Di Martino & Taylor (2013). It is also within the size range of an undescribed species of *Idmonea* from the Bathonian–Callovian of Balin, Poland (Taylor 2009). However,

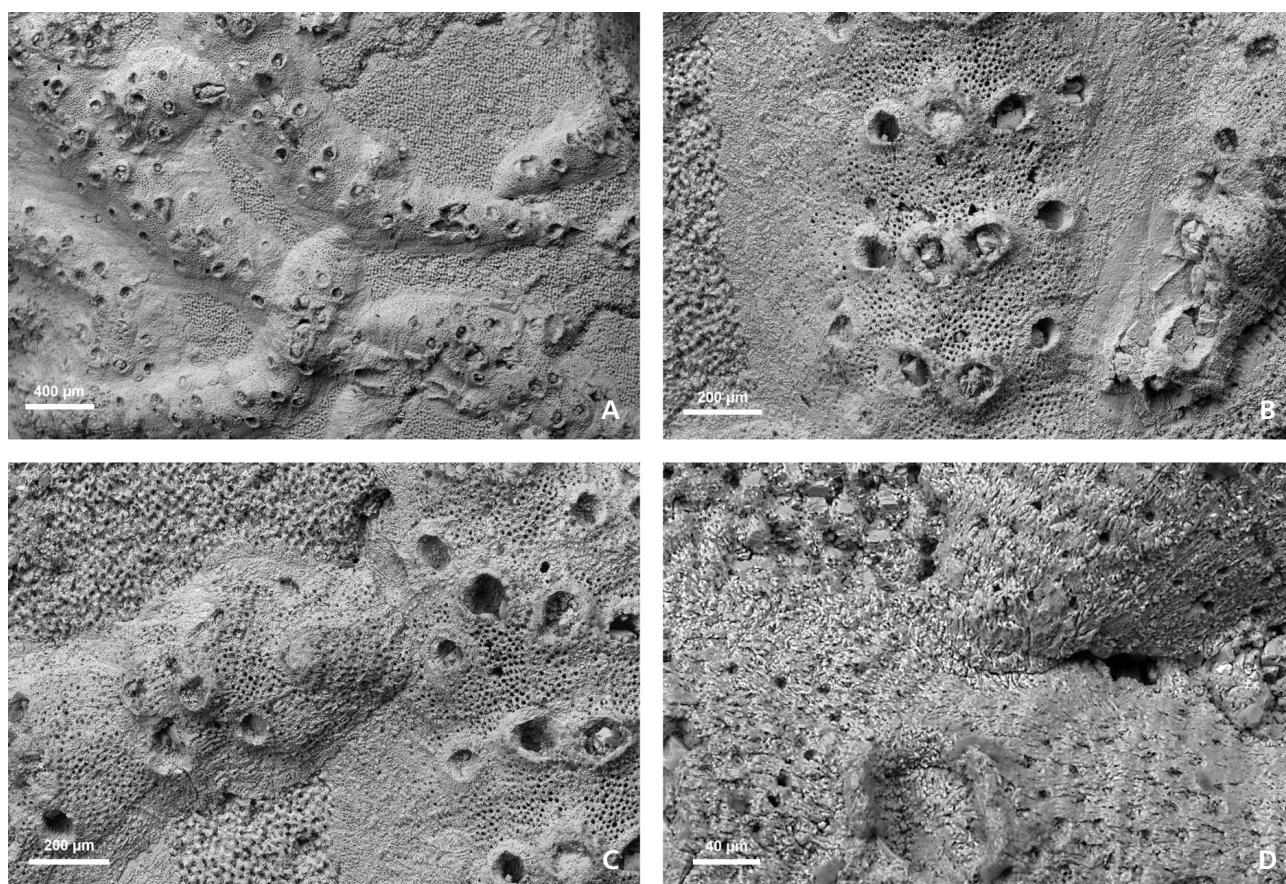


Figure 6. *Idmonea snehi* sp. nov. encrusting a crinoid pluricolumnal from the Matmor Formation (Callovian) of Hamakhtesh Hagadol, southern Israel, NHMUK BZ 7726. • A – colony showing lateral branching pattern; B – branch with selvedge made of kenozooids; C – budding point of lateral branch; D – closer view of budding point showing shapes of pseudopores.

the presence of lateral branching, which is profuse in *I. snehi*, distinguishes the new species from all Jurassic species of *Idmonea*. Indeed, the customary terminal branching seen in *Idmonea* seems to be lacking in the new species, to be replaced entirely by lateral branching. The lateral branching pattern of *Idmonea snehi* is the earliest example of lateral branching in a post-Palaeozoic cyclostome, and the only published example of lateral branching in any Jurassic bryozoan. Worn lateral branch origins show the branches emerge from an aperture in the outermost row of autozooids.

Occurrence. – C/W-247 and C/W-602 (Table 1).

Family Plagioeciidae Canu, 1918

Genus *Hyporosopora* Canu & Bassler, 1929

Type species. – *Hyporosopora typica* Canu & Bassler, 1929; Bathonian of Calvados, France.

Hyporosopora nana sp. nov.

Figure 7A–D

Types. – Holotype: NHMUK BZ 7727(c) (Fig. 7A, B, D). Paratypes (on the same substrate as holotype): NHMUK BZ 7727(a), BZ 7727(b) (Fig. 7C).

Type locality. – C/W-371; Matmor Formation (Middle Jurassic, Callovian, upper *Peltoceras athleta* Zone) in the Matmor Hills near the centre of Hamakhtesh Hagadol in southern Israel (Table 1).

Type horizon. – Subunit 51 (see Goldberg 1963) of the Matmor Formation, approximately 28 metres above the base of the unit.

Etymology. – The Latin *nana* means small. It is used here in reference to the very small autozooids in this species.

Material. – Several specimens but only the holotype and one paratype are fertile with diagnostic gonozooids.

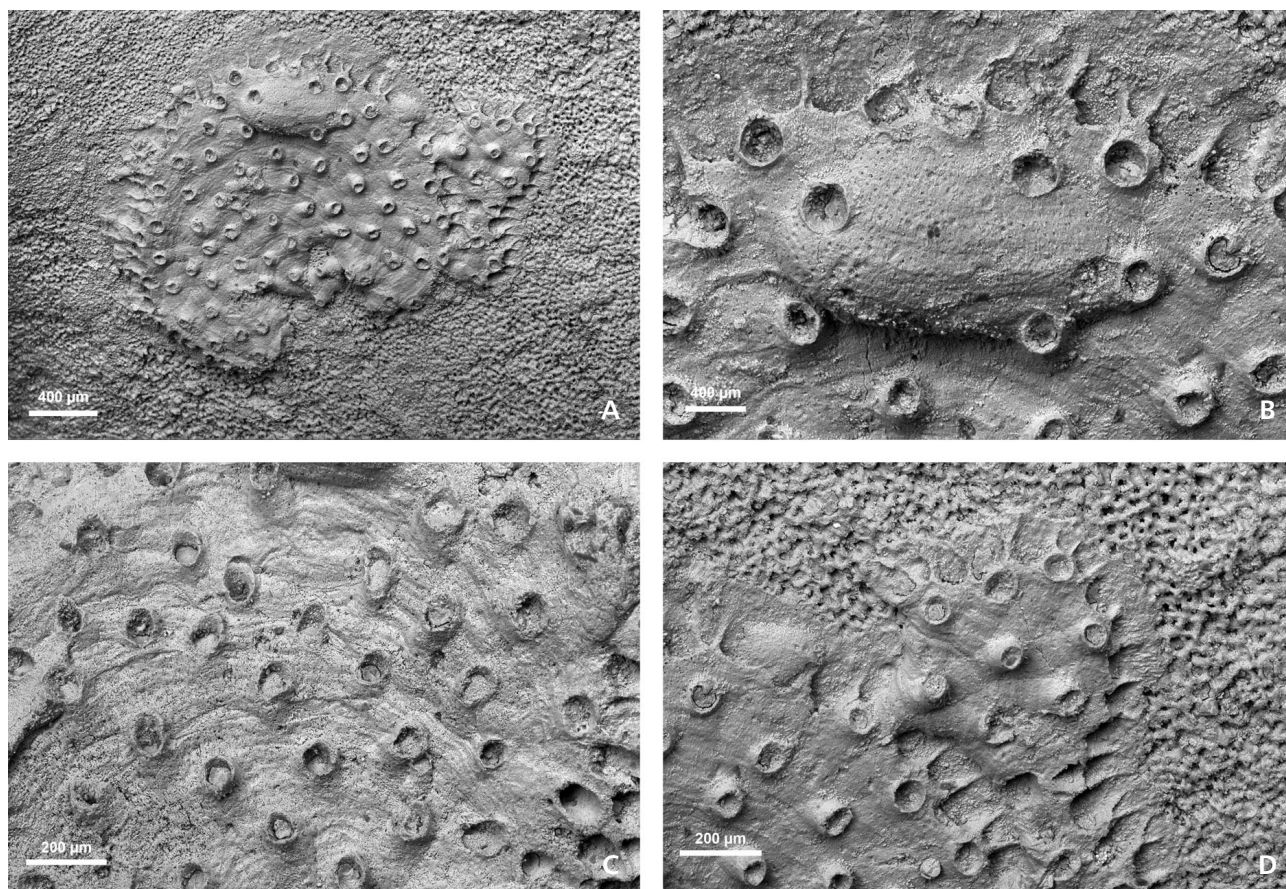


Figure 7. *Hyporosopora nana* sp. nov. encrusting a crinoid holdfast from the Matmor Formation (Callovian) of Hamakhtesh Hagadol, southern Israel. • A – complete colony showing ancestrula, gonozooid and subcolonies on the right, NHMUK BZ 7727(c); B – gonozooid with oeciopore at the distal end, NHMUK BZ 7727(c); C – autozooid frontal walls with pseudopores, NHMUK BZ 7727(b); D – subcolony budding from periphery of main colony, NHMUK BZ 7727(c).

Measurements. – All measurements are from the holotype. Autozooid frontal wall width 0.05–0.07 mm (mean = 0.06 mm; $n = 8$); frontal wall length 0.20–0.30 mm (mean = 0.24 mm; $n = 11$); longitudinal aperture diameter 0.02 to 0.05 mm (mean = 0.03 mm; $n = 15$); transverse aperture diameter 0.01–0.04 (mean = 0.02 mm; $n = 15$). Gonozooid length 0.02 mm, width 0.31 mm; oeciopore longitudinal aperture diameter 0.02 mm, latitudinal aperture diameter 0.02 mm.

Description. – Colony encrusting, sheet-like, multiserial, unilamellar, ovoidal (Fig. 7A); subcolonies branching from distal growing edge of parent colony which is low and exposes one generation of buds (Fig. 7D). Autozooids small, with slightly convex frontal walls crossed by transverse growth lines; shallow indentations at zooidal boundaries; apertures small subcircular or longitudinally ovoidal; peristomes short or broken; terminal diaphragms often present; pseudopores circular (Fig. 7C, D). Gonozooid transversely ovoidal (Fig. 7B), margins indented by a few autozooidal apertures; oeciopore diameter at small end of autozooid

transverse aperture diameter range; pseudopores circular and dense across gonozooid surface (Fig. 7B). Ancestrula about 0.28 mm long, damaged in the single known example but with aperture estimated to be 0.05 mm in transverse diameter and protoecium 120 µm wide.

Discussion. – *Hyporosopora nana* is similar to *H. tenera* (Reuss, 1867) as described by Taylor (2009) and Zatoń & Taylor (2009) from the Middle Jurassic of Poland. *H. nana* and *H. tenera* both have elliptical gonozooids, as well as the same general colony shape. *H. nana*, however, has considerably smaller autozooidal frontal wall widths of 0.05 to 0.07 mm, compared to 0.11–0.14 mm in *H. tenera* (see also Zatoń *et al.* 2013). Zatoń & Taylor (2009) reported an oeciopore length of 0.066 mm and width of 0.091 mm for *H. tenera*, whereas *H. nana* has a significantly smaller oeciopore length of 0.02 mm and width of 0.02 mm. The same pattern holds true for all other measurements as well. *H. nana* has the smallest zooids in the Matmor *Hyporosopora* assemblage, as well the smallest so far identified in the literature for the genus.

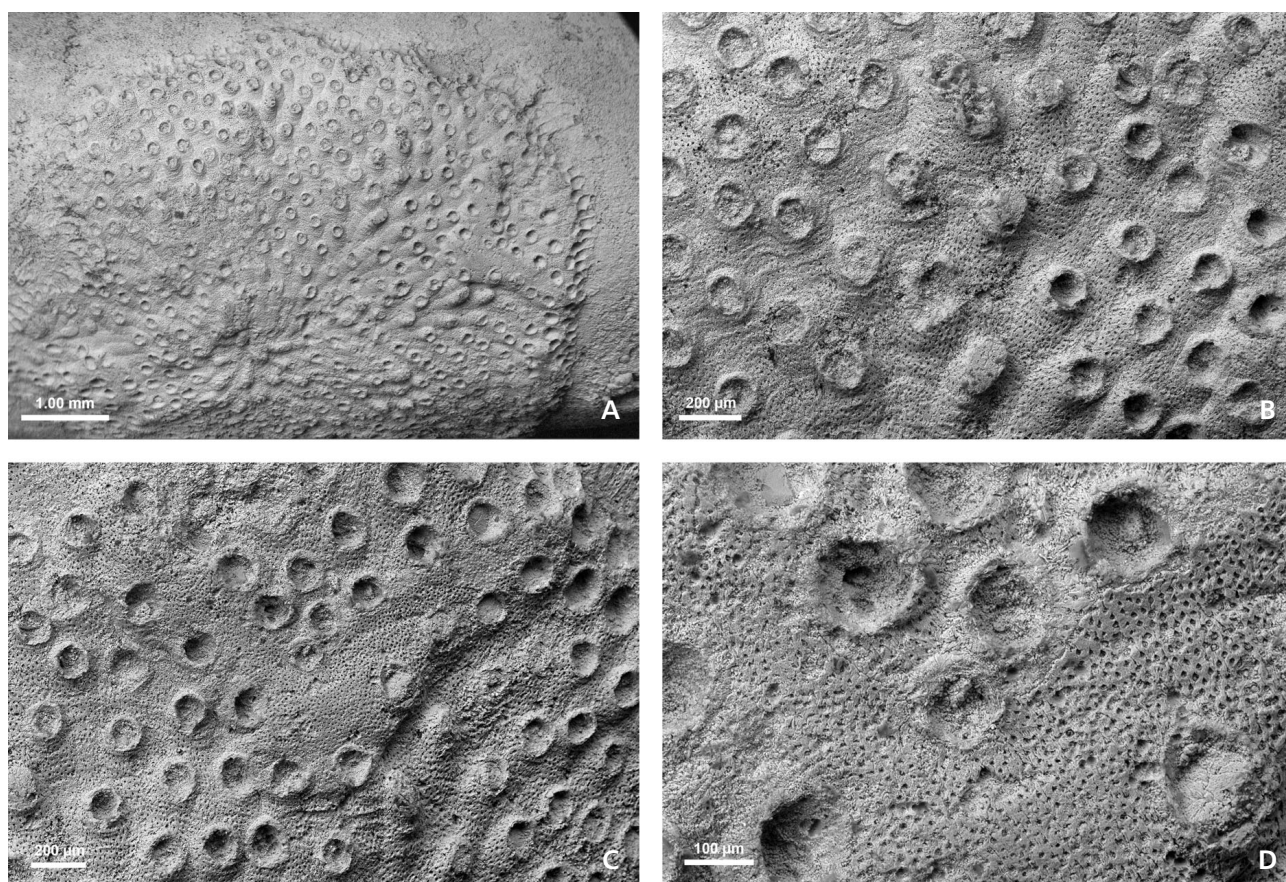


Figure 8. *Hyporosopora negevensis* sp. nov. encrusting a crinoid pluricolumnal from the Matmor Formation (Callovian) of Hamakhtesh Hagadol, southern Israel, NHMUK BZ 7728. • A – complete colony showing gonozooid; B – autozooids with pseudopores; C – boomerang-shaped gonozooid with ooeciopore at the junction of the two arms; D – closer view of ooeciopore and pseudopores in Fig. 8C.

Occurrence. – C/W-371 and C/W-602 (Table 1).

***Hyporosopora negevensis* sp. nov.**

Figure 8A–D

Types. – Holotype: NHMUK BZ 7728 (Fig. 8).

Type locality. – C/W-609; Matmor Formation (Middle Jurassic, Callovian, upper *Peltoceras athleta* Zone) in the Matmor Hills near the centre of Hamakhtesh Hagadol in southern Israel (Table 1).

Type horizon. – Subunit 51 (see Goldberg 1963) of the Matmor Formation, approximately 28 metres above the base of the unit.

Etymology. – The species name *negevensis* refers to the type locality in the Negev Desert.

Material. – Several specimens but only the holotype is fertile (NHMUK BZ 7728).

Measurements. – All measurements are from the holotype. Autozooid frontal wall width 0.10 to 0.16 mm (mean = 0.13 mm; $n = 20$); frontal wall length 0.33–0.44 mm (mean = 0.36 mm; $n = 12$); longitudinal aperture diameter 0.06–0.10 mm (mean = 0.09 mm; $n = 30$); transverse aperture diameter 0.05–0.10 (mean = 0.08 mm; $n = 35$). Brood chamber length of median axis (to the ooeciopore) is 0.60 mm; distal width of brood chamber is 1.87 mm; ooeciopore longitudinal aperture diameter 0.07 mm, latitudinal aperture diameter 0.05 mm.

Description. – Colony encrusting, sheet-like, multiserial, unilamellar, ovoidal. Growing edge shallow, usually revealing only one generation of buds. Autozooids moderately large, with slightly convex frontal walls crossed locally by transverse growth lines; boundary walls marked by slight grooves; apertures crowded, longitudinally ovoidal, some closed by terminal diaphragms; peristomes short or abraded; pseudopores teardrop-shaped. Gonozooid boomerang-shaped with ooeciopore at base of the two lateral lobes; ooeciopore circular, slightly smaller than an autozooidal aperture; pseudopores dense.

Discussion. – *Hyporosopora negevensis* is similar to *H. radomensis* described by Hara & Taylor (2009) from the Polish Kimmeridgian; both have boomerang-shaped gonozooids; however, the measurements of the gonozooid length and width, as well as the size of the ooeciopore, differ. The frontal wall widths of *H. radomensis* autozooids are reported as 0.105–0.180 mm. The frontal wall widths of *H. negevensis* are 0.098–0.163 mm, which is smaller than *H. radomensis*, though with some overlap. The frontal wall lengths are appreciably different: 0.520–0.840 mm in *H. radomensis* vs 0.331–0.435 mm in *H. negevensis*. The pseudopores on the autozooids of the Matmor species are much more densely packed than on *H. radomensis* (Hara & Taylor, 2009, p. 572, fig. 10c), and they are circular rather than drop-shaped or crescent-shaped as in *H. sauvagei*.

Occurrence. – C/W-609 (Table 1).

Discussion and conclusions

The tropical Matmor bryozoan fauna resembles other Middle Jurassic assemblages in that it has the three encrusting colony-forms typical of Jurassic bryofaunas: uniserial branching runners (here as *Stomatopora*), oligoserial branching ribbons (*Oncousoecia* and *Idmonea*) and multiserial sheets (*Hyporosopora* and *Microeciella*). In this sense the fauna is very similar at generic level to those from the temperate Middle Jurassic of Europe, e.g., Poland (Taylor 2009, Zatoń & Taylor 2010, Zatoń *et al.* 2013). However, at the species level the Matmor bryozoans are distinct: of the six species described here, four are new.

The diversity and abundance of the Matmor bryozoan fauna warrant discussion. Despite over a decade of intense collecting, only the six species described here have been found, and most within a single marl-rich unit in the formation. Taylor & Ernst (2008) noted that the Middle Jurassic was a time when bryozoan diversity was only just beginning to recover from the long-lasting effects of the end-Permian, and possibly the late Triassic, extinction events. Bryozoan assemblages from the Middle Jurassic are the most diverse of the period, with an average species richness of 5.2 and a median of 17 per assemblage. The Matmor bryozoan assemblage matches Taylor & Ernst's (2008) average, but it falls well short of the median of 17 species. The bryozoan assemblages in Poland easily meet and many exceed the Middle Jurassic average and median (Taylor 2009, Zatoń & Taylor 2009, Zatoń *et al.* 2013). The Bathonian bryozoan assemblage in the Carmel Formation of southern Utah, USA, contains only seven cyclostome species and thus has a similar species richness, but the abundance of bryozoans there is far greater (Taylor & Wilson 1999). The Carmel fauna was also more environmentally restricted as indicated by an almost total lack of

brachiopods (there are only a few thecideides) and echinoderms.

Our hypothesis is that the Matmor bryozoans were less diverse and abundant than their temperate equivalents because they lived in an oligotrophic, tropical environment (as supported by the abundance of corals in the Matmor Formation; see Hallock *et al.* 1988, and references therein). Taylor & Allison (1998) showed that bryozoans are insignificant contributors of sediment in the post-Palaeozoic tropics, reflecting their small biomass. This contrasts with their significant contribution to Palaeozoic tropical sediments. There are far too few data points to discuss a Jurassic latitudinal trend for bryozoan diversity, but it is worth noting that the Matmor fauna in the Middle East was on the southwestern flank of the Tethys Ocean almost directly south of Europe with no land barriers between the living communities. Zatoń *et al.* (2013) described 22 cyclostome species from a single Callovian locality in Poland, which is almost four times more than the diversity of the Callovian cyclostomes in this Israeli fauna.

All of the Matmor bryozoan genera are known from earlier and later Jurassic occurrences, so this tropical fauna does not seem to represent either a “cradle” or “a museum of biodiversity” for the cyclostomes (Jablonski *et al.* 2006, p. 102). However, *Idmonea snehi* in this assemblage is the first occurrence of lateral branching among cyclostome bryozoans, and thus far the only Jurassic example. Most encrusting cyclostomes exhibit terminal branching whereby bifurcation at distal growing tips causes branch multiplication. In contrast, lateral branches originate from the sides of existing branches, proximal of the growing tips. This process requires either skeletal resorption, as proposed by Harmelin (1976), or the retention of an uncalcified patch behind the advancing growing tip from which budding to produce a lateral branch can later be activated. The latter appears to be the case in *I. snehi* where the lateral branches seem to emerge from autozooidal apertures. The oldest example of lateral branching in a cyclostome is recorded in *Cuffyella arachnoidea* (Hall, 1847), a palaeotubuliporine common in the Cincinnati (Late Ordovician) of the US mid-west (Taylor & Wilson 1996). Until the discovery of *I. snehi* from the Callovian, this style of branching was thought not to reappear in cyclostomes until the Early Cretaceous (Hauterivian) from where Jablonski *et al.* (1997, p. 519) recorded its occurrence in an un-named species of the uniserial tubuliporine *Voigttopora*.

Jurassic encrusting bryozoans are most commonly found in cryptic spaces such as the undersides of corals and sponges or the interiors of bivalves (Taylor & Ernst 2008). Previous observations of the Matmor bryozoans (Wilson *et al.* 2008, 2010) suggested that they too were mostly cryptic, but the thorough survey in this work shows that instead the majority lived on exposed surfaces. Out of the 130 colonies examined, all but a few encrusted upward-facing sur-

faces of echinoderm ossicles that were sitting on top of marl-rich sediments. There are numerous corals and sponges in this same unit with cryptic undersurfaces encrusted by serpulids, sabellids and thecideide brachiopods, but bryozoans are nearly absent there (Wilson *et al.* 2008, Vinn & Wilson 2010). This is a very Palaeozoic-like microenvironmental distribution similar to the bryozoans that encrusted exposed crinoid calyxes and stems in the Silurian Waldron Shale of Indiana, USA (Liddell & Brett 1982).

The Matmor bryozoans, especially *Hyporosopora*, have significantly smaller zooids than their temperate equivalents in Europe (see Systematics section above). This appears to be an example of the “temperature-size rule” where temperature and size have an inverse relationship as shown by many ectotherms (Atkinson 1994). The relationship has been studied extensively in a laboratory setting among conspecific colonies of modern cheilostome bryozoans: “Temperature consistently provides, either directly or indirectly, a pervading and dominant influence on zooid size” (Okamura *et al.* 2011, p. 144). While most data concerns temperature-related differences in zooid size within cheilostome species, or even within colonies, there are indications that the relationship may also operate between species of the same genus (Kukliński & Taylor 2008) and among stenolaemates too (Jiménez-Sánchez *et al.* 2013). Therefore the small zooid sizes of the Matmor cyclostome species may be a function of their development on a warm, tropical shelf. This is in contrast to the larger zooids typifying congeneric bryozoan species growing in the cooler, temperate waters of Europe (Taylor & Wilson 1999, Hara & Taylor 2009, Zatoń *et al.* 2013).

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