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New discoveries in Eastern Mediterranean mesophotic sponge grounds: updated checklist and description of three novel sponge species

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Abstract

Rich and diverse mesophotic sponge grounds were recently discovered along the easternmost part of the Mediterranean Sea (Israeli coast). Seven sites have been surveyed over the last decade (2009-2019) and the sponge specimens discovered and collected in these expeditions have increased the known sponge richness of the Israeli fauna by ~34%. Here we provide an updated checklist along with the distribution of the various species in seven mesophotic sponge grounds along the coast. Nine mesophotic species have been added, seven of which are new to the Israeli coast. Moreover, we describe three novel species: *Hemiasterella verae* sp. nov., *Axinella venusta* sp. nov., and *Plakortis mesophotica* sp. nov. *H. verae* sp. nov. differs from other congeneric species in both shape and color; in addition, it has thinner megascleres with more abundant oxeas and microscleres containing both oxyasters and strongylasters. *A. venusta* sp. nov. is a rather stiff and smooth axinellid with only a few short protruding spicules, and differs from other congeneric species mainly in shape and color. *P. mesophotica* sp. nov. is characterized by many folds and grooves, and molecular analysis revealed only a 96% similarity with *Plakorits simplex*.The discovery of these novel species highlights the importance of studying ecosystems that are not readily accessible. Further research of these mesophotic sponge grounds is needed in order to establish the community baseline data and support conservation attempts for these unique habitats.

Keywords: New species; checklist; Levantine Sea.

Introduction

Sponge richness and diversity in the Mediterranean Sea are considered to decrease along a NW to SE gradient (Voultsiadou, 2005a). The Levantine Sea, being the easternmost part of the Mediterranean, has been considered to be the poorest area (Voultsiadou, 2005b, 2009; Coll *et al.*, 2010; 2012; Mouillot *et al.*, 2011). While this is thought to be mainly due to a gradient in environmental factors, at least part of the decrease can be attributed to the differences in research efforts in the different parts of the Mediterranean Sea (Vacelet *et al.*, 2007; Voultsiadou, 2009; Gerovasileiou & Voultsiadou, 2012; van Soest *et al.*, 2012). In accordance, each new study of sponges in the Levant has resulted in the discovery of species new to the region, and in many cases the description of species novel to science (Lévi, 1957; Tsurnamal, 1969; Vacelet *et al*., 2007; Vacelet & Pérez, 2008; Evcen & Çinar, 2012). Moreover, with recent technological advancements, it is now easier to reach previously inaccessible habitats, such as caves and mesophotic to abyssal depths (Lesser *et al.*, 2009; Gerovasileiou & Voultsiadou, 2012; Cerrano *et al.*, 2019). These advances have indeed led to the discovery of new species (Cerrano *et al*., 2019; Pomponi *et al.*, 2019). The mesophotic surveys conducted along the Israeli coast between 2009 and 2015 have added 25 species to the Israeli fauna, at least 12 of which are new to the Levantine Sea (Idan *et al*., 2018). Furthermore, as many of the sponge species in the mesophotic zone are small-sized, cryptic, encrusting, and difficult to sample by Remotely Operated Vehicles (ROV), it is likely that the sponge biodiversity in the mesophotic zone is underestimated (Fig. 1). It is therefore of high importance to find ways by which to sample in these unique habitats (Bo *et al.*, 2012; Sitja & Maldonado, 2014; Bertolino *et al.*, 2015; Idan *et al.*, 2018), and even more so in areas such as the Levantine Sea, where the abiotic conditions in the shallow zone are harsh, and the mesophotic zone may

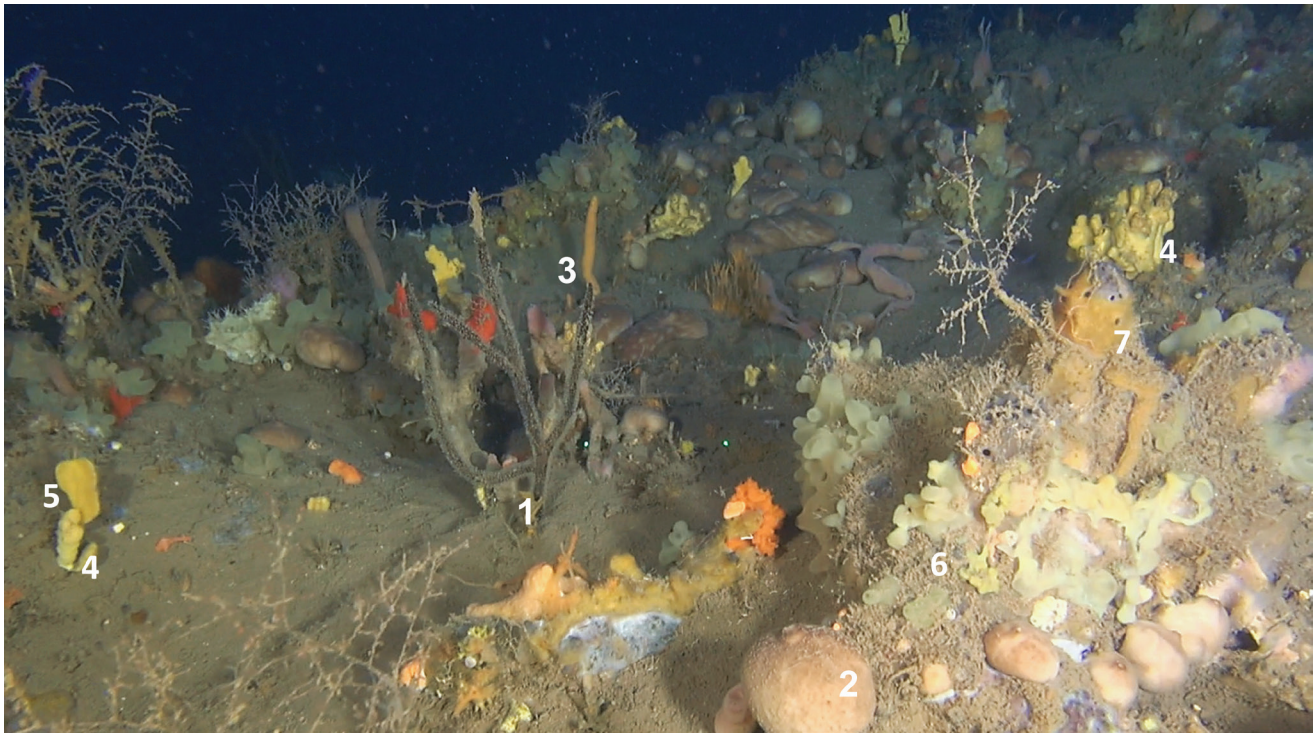

Fig. 1: Typical view at the Herzliya site, 97 m depth. The following species can be noticed: 1. *Raspailia (Raspailia) viminalis*, 2. *Chondrosia reniformis*, 3. *Axinella polypoides,* 4. *Axinella damicornis*, 5. *Axinella venusta* sp. nov, 6. *Oscarella tuberculata*, 7. *Fasciospongia cavernosa* (covered by *Oscarella tuberculata* and, and several encrusting sponges).

contain a considerable part of the local richness (Idan *et al*., 2018). In this study, we present an updated checklist and species distribution for seven mesophotic sponge grounds surveyed along the Israeli coast, as well as a description of three species collected during the mesophotic expeditions that are proposed as novel species in the genera: *Axinella*, *Hemiasterella*, and *Plakortis*.

Materials and Methods

Sampling

Sponges were collected from the mesophotic sponge grounds at a depth of 80-130 m, off the Israeli Mediterranean coast (Table 1, Fig. 2). Collections were carried out on-board the R/V Mediterranean Explorer using an ROV (ECA-Robotics H800). The ROV was equipped with a five-function-manipulator, a full high-definition camera, and two parallel laser beams for scale. Collected samples were documented and an initial morphological description was given on board. The specimens were photographed *in situ* (underwater) prior to collection, and again in the laboratory, after which they were preserved in 85% and 100% ethanol for morphological and molecular taxonomic evaluation, respectively.

Morphological identification

Preparation of spicules and tissue sections followed standard methods (Hooper, 2003). In some cases, spicules and tissue were examined using scanning electron microscopy (SEM). The spicule composition was analyzed for each sample according to Rützler & Macintyre (1978). For each spicule type, the length and width were measured and the size range, mean, and standard deviation were calculated (n = 30 per sample). For classification and identification, we followed Hooper & van Soest (2002), Morrow & Cárdenas (2015), and the updated nomenclature reported in the World Porifera Database (van Soest *et al.*, 2021).

Molecular identification

DNA was extracted with the DNeasy kit (Qiagen #69504) following the manufacturer's protocol (for elution of the DNA we used only 40-60 µl of elution buffer). For the molecular identification we amplified and sequenced fragments from the 28S and 18S rDNA as well as the mitochondrial COI (the barcoding region) commonly used for sponge phylogeny (Cardenas *et al.*, 2012). The choice of molecular markers to amplify for species identification was based on data available for comparison in GenBank, or on PCR success. The 18S rDNA gene was amplified using the primer sets 18S1/18S2 (Borchiellini *et al.*, 2001). The 28S rDNA gene was amplified using the primer sets C1' modified/D2 (Chombard *et al.*, 1998) or C1' modified/28S_R1t (Idan *et al*., 2018). The COI gene was amplified with the primers LCO1490 (Folmer *et al*., 1994) and COX1R1 (Rot *et al*., 2006).

The obtained sequences were compared with those in the nucleotide database of the National Center for Biotechnology Information (NCBI), using BLAST search (BLASTN 2.5.0+; Zhang *et al.*, 2000).

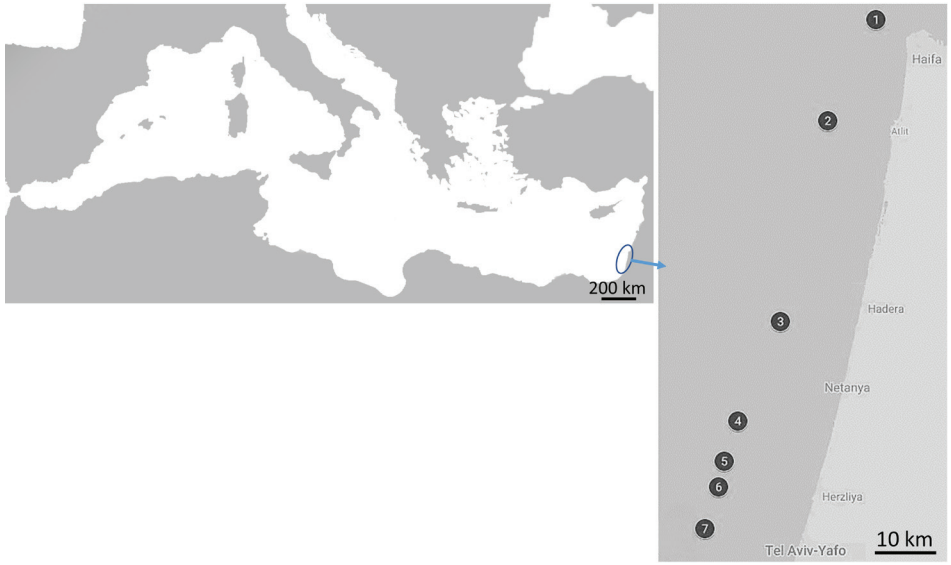

Fig. 2: A. Map of the Mediterranean Sea, the coast of Israel is marked by a blue circle. B. Map of the sampling sites along the Israeli coast. Site numbers correspond with Table 1.

Table 1. The study sites and their characteristics.

#	Site	Formation	Depth range (m)	Coordinates
1	**Haifa – Rosh Carmel**	Extension of a terrestrial limestone ridge	80-130	32.875417º N, 34.861972º E
2	**Atlit**	Submerged sandstone ridge	99-120	32.741611º N, 34.839306º E
3	**Hadera**	Submerged sandstone ridge	96-106	32.415611º N, 34.738764º E
4	**Nethanya**	Submerged sandstone ridge	107-120	32.271481º N, 34.666167º E
5	**Shefayim**	Submerged sandstone ridge	95-123	32.214222º N, 34.643228º E
6	**Herzliya**	Submerged sandstone ridge	92-127	32.176250º N, 34.633056º E
7	**Tel Aviv**	Submerged sandstone ridge	93-117	32.149694º N, 34.623750º E

Results and Discussion

Class Demospongiae, 1978
Order Tethyida Morrow & Cárdenas, 2015
Family Hemiastrellidae Lendenfeld, 1889
Genus *Hemiasterella* Carter, 1879
***Hemiasterella verae* sp. nov.**

Material examined. Holotype - Po.25931, site Herzliya, 97 m depth, date 28.07.15. Paratype - Po. 26354, site Herzliya, 99 m depth, date 04.07.18. Collection site: 32.176250º N, 34.633056º E.

Description. External morphology: The two specimens collected are small, massive-columnar. The holotype pieces measure between 1.4 x 3.4 x 3.8 - 1.6 x 0.8 x 0.6 cm and the paratype is 3.7 x 1.7 x 1.2 cm (Fig. 3 A, B, respectively). The surface shows irregular folds with grooves generally running parallel to the longest body axis. The surface is hispid with sparse long spicules protruding the surface (Fig. 4). Color: surface is yellow-orange in life (Fig. 3 A, B) and creamy-white after preservation in ethanol. The internal part of the sponge is yellow-cream.

Skeleton. Columns and cross-connections of the megascleres create a plumoreticulated structure. Some megascleres protrude from the ectosome, causing hispidation of the surface. Columns are surrounded by highly abundant asters. Aster density gradually increases towards the sponge surface (Fig. 4).

Spicules. Megascleres are mainly slightly curved, curved, or flexuous styles, measuring 1350-1825 x 7.5-17.5 µm (Table 2, Fig. 5 J-M). The round head of the styles may also be strongyloxea fashion; the pointing end is regularly acerate or stepped. Rare oxea (or modified styles), were found in both individuals, measuring 1157-1775 x 5-15 µm, most with one end hastate or blunt while the other end was stepped or acerate (Table 2). Microscleres: oxyaster and strongylasters ranging from 12-27 µm in total diameter, with 3-11 pointed to blunt spiny rays (Table 2, Fig. 5 A-I). Spines are more abundant towards the tip of the ray; length of rays was normally equal. Asters with fewer rays were typically larger (Fig. 3 C, D, Fig. 5 A-I).

Molecular. 28S and 18S were sequenced. GenBank accession number: 18S - KX866780, 28S - MW380746,

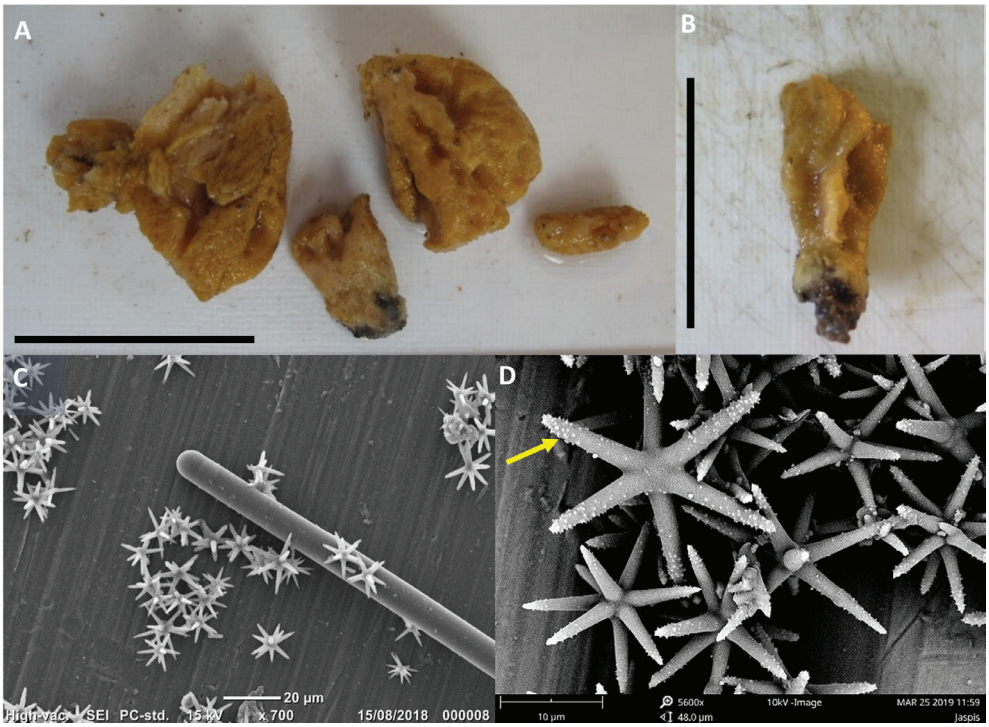

Fig. 3: *Hemiasterella verae* sp. nov. morphological characteristics. A. *H. verae* sp. nov. holotype; B. *H. verae* sp. nov. paratype, scale bar A, B 5 cm; C. A style and euasters with different numbers of rays; D. Oxyasters with different numbers of rays, spines are visible on the rays (arrow).

for Po.25931 and GenBank accession number: 18S - MW380748, 28S – MW380747 for Po.26354. Currently, there are no other 18S sequences of *Hemiasterella* in GenBank, a maximum-likelihood phylogenetic tree for 18S can be found in Idan *et al*. (2018), where *H. verae* is referred to as *Jaspis* sp. Sequences of the 28S large subunit ribosomal RNA gene were therefore submitted to a BLAST search against sponge sequences in general, and specifically against Hemiasterellidae sequences, based on the rearrangements in *Hemiasterella* taxonomy by Morrow *et al*. (2018, 2019). Hemiasterellidae sequences and others sponge 28S sequences that were >94% identical to the *H. verae* sequence in the BLAST search were aligned using MAFFT (Katoh *et al*., 2005). The alignment was corrected by eye, and short sequences of *Adreus micraster* (accessions AY561903 and AY626306) and *Stelligera stuposa* (accessions AY561950 and AY626321) were assembled to create a sequence that covers most of the length of the alignment. A maximum-likelihood phylogenetic tree was reconstructed with PhyML (Guindon *et al*., 2010) using the GTR substitution model (Fig. S1). The 28S sequence of *H. verae* formed a cluster with three *Hemiasterella* sequences (Fig. S1). It was clustered with Hemiasterellidae sequence originated from the USA (Thacker *et al.*, 2013) with a bootstrap support of 82. Two other sequences of *Hemiasterella* sp. clustered with low bootstrap support, however the country of origin of these samples was not provided (Nichols, 2005). It is important to note that sequences of *Hemiasterella* herein identified to the species level do not exist in the GenBank.

Distribution and ecology notes. *Hemiasterella verae* sp. nov. was found on two pinnacles in the Herzliya mesophotic sponge grounds. In both cases the specimens were not intentionally collected but found among or attached to other species that we sampled. The holotype found in the collection basket together with *Axinella damicornis*, *Dictyonella incisa*, *Sarcotragus foetidus*, *Coscinoderma sporadense*, *Aplysina cavernicola* and *Plakortis mesophotica* sp. nov. The paratype was attached to a piece of substrate together with *Chondrosia reniformis*. Due to the small size of this species, we were not able to detect it in the images taken underwater, making it hard to assess its distribution at other mesophotic sites.

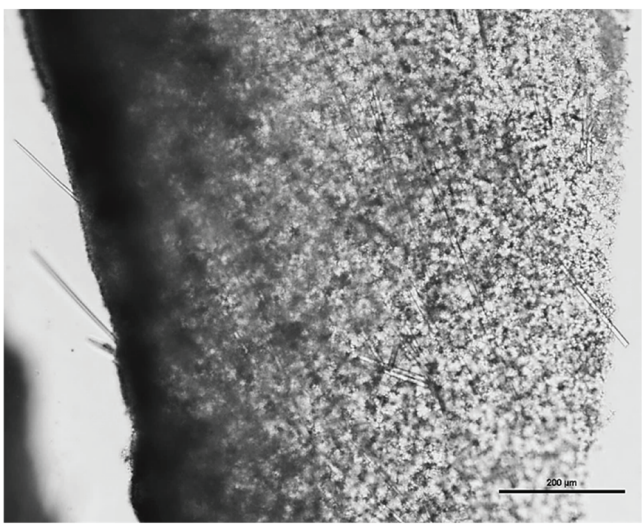

Fig. 4: Skeletal structure of *Hemiasterella verae* sp. nov. longitudinal section of holotype (scale: 200 µm). The euasters in the image appear as dark spots, as their density increase the section becomes darker.

Taxonomic remarks. This sponge is assigned to the

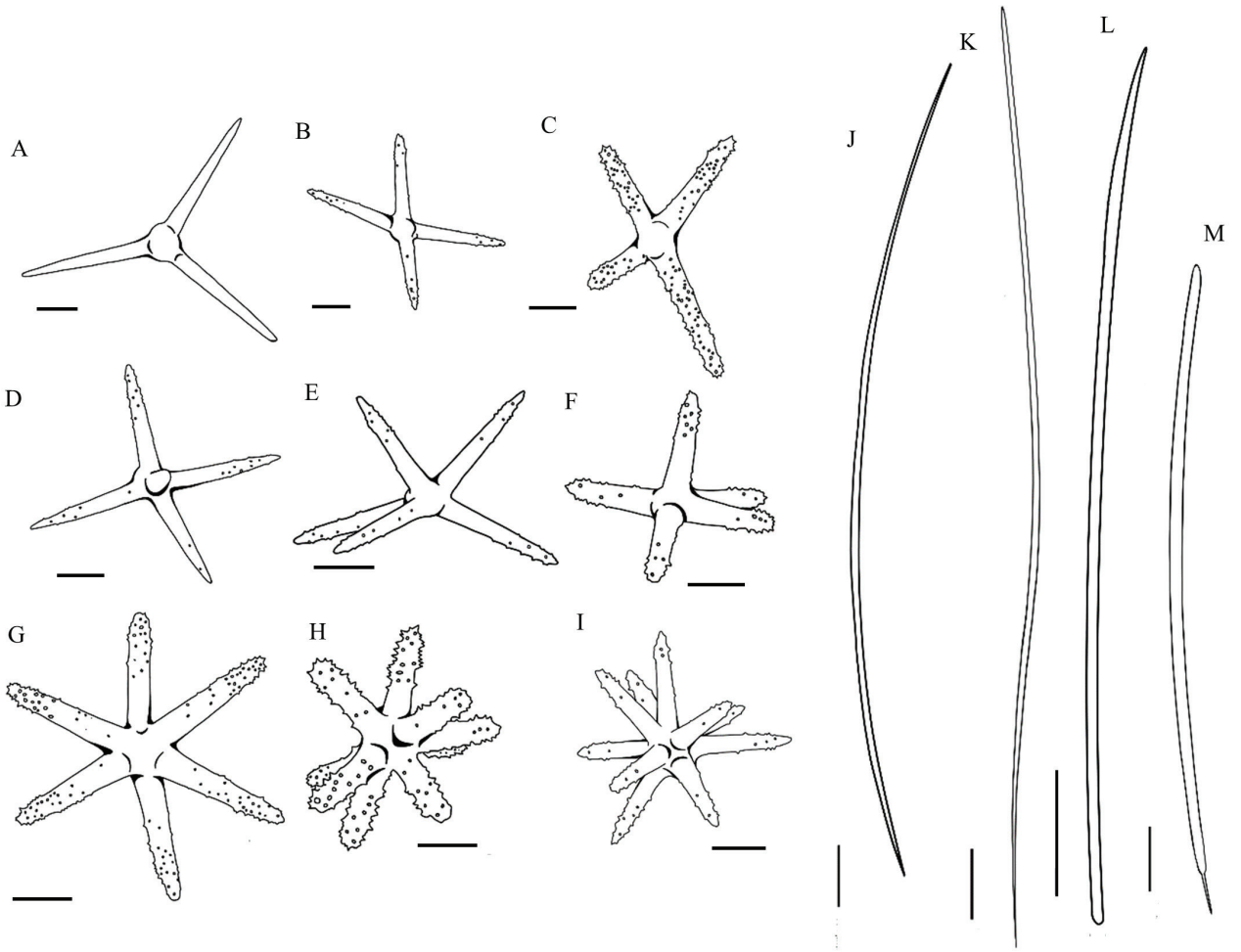

Fig. 5: Spicules of *Hemiasterella verae* sp. nov.: A-B. Oxyasters; C. Strongylasters; D-E. Oxyasters; F-H. Strongylasters; I. Oxyasters, scale bar 5µm; J-K. Oxeas; L-M. Styles, scale 100 µm. Figure drawn by Michelle Dan.

Table 2. Comparison of morphological characteristics of *Hemiasterella* spp. recorded from the Mediterranean Sea.

	H. aristoteliana **Voultsiadou-Koukoura & van Soest, 1991***	***H. elongata*** **Topsent, 1928***	***H. verae*** **sp. nov.**			
		ZMA specimen	Original	Alboranian specimens	Holotype	Paratype
Specimen size	3.5 x 1 cm	Not specified	Not specified	0.5-1.5 x 0.4-0.7 cm	The sponge arrived in pieces of 3.7 x 4.1-1.8 x 0.66 cm	3.1 x 1.72
Styles (µm)	1800-3000 x 18-37	550-1800 x 22-36	1500-2000 x 25-60	1316-2250 x 10-30	1350-1825 x 7.5-17.5	926-1543 x 6-14
Oxea (µm)	No	Rare 600-1500	Rare 1900-2345	1825 x 10	1150-1775 x 5-15	1375 x 11
Diameter of asters (µm)	13-42	12-18	15-18	14-23	12-27	12-29
No. of aster rays	1-12	8-13	12	10-15	3-11	3-12

**H. aristoteliana* (Voultsiadou-Koukoura & van Soest, 1991), *H. elongata* (Sitja & Maldonado, 2014; Topsent, 1928).

genus *Hemiasterella* because it has mainly styles as megascleres and oxyasters as microscleres. Unlike most of the species in this genus, this sponge does not display the typical vase form. Two other species with a similar morphology are known from the Mediterranean Sea: *H. aristoteliana* Voultsiadou-Koukoura & van Soest, 1991, from the Aegean Sea (Voultsiadou-Koukoura & van Soest, 1991); and *H. elongata* Topsent, 1928, from the Alboran Sea (Sitja & Maldonado, 2014; Topsent, 1928). The external morphology of *H. verae* sp. nov. differs in size and color from that of *H. elongata*. The latter is much smaller and described as bright to creamy white, while *H. verae* sp. nov. is orange. Although the color of *H. verae* sp. nov. is similar to that of *H. aristoteliana*, its shape is more massive and not branched like the latter. The spicules of *H. verae* sp. nov. also differ from those of *H. elongata* and *H. aristoteliana* (Table 2); its styles are slenderer than those of *H. elongata* and *H. aristoteliana*, and its oxeas are more abundant than described for *H. elongata* (Sitja & Maldonado, 2014). While the diameter of the asters may also fit *H. elongata*, the euasters in *H. verae* sp. nov. were comprised of both oxyasters and strongylasters, and the number of rays demonstrated a greater variation. The number of rays was similar to that of *H. aristoteliana*, but the latter only has strongylasters.

Etymology. The species name *verae* is given in honor of Vera Idan, a brave Holocaust survivor.

Class Demospongiae, 1978
Order Axinellida
Family Axinellidae Carter, 1875
Genus *Axinella* Schmidt, 1862
***Axinella venusta* sp. nov.**

Material examined. Holotype – Po. 25779, site Herzliya, 97 m depth, date 23.10.13, collection site: 32.176111ºN, 34.632778ºE, Paratype – Po. 26035, site Herzliya, 98 m depth, date 24.03.16, collection site: 32.176250º N, 34.633056º E.

Description Both specimens are erect with a small peduncle; the holotype is larger and foliaceous (size 10.5 cm x 4.5 cm); the paratype is smaller and flabellate (5 cm x 2.7 cm). This difference in form may be due to the paratype's small size, which might not have reached its fully developed form (Fig. 6A, 7B). The surface is uneven, somewhat rugose, and slightly hispid, with a few short spicules protruding through a "skin"-like membrane covering the surface (Fig. 7 A). Color: bright yellow-orange in life and creamy-white after preservation in ethanol (Fig. 6 A-B, Fig. 7). Sponge consistency is stiff and not compressible.

Skeleton. A plumoreticulated skeletal arrangement is clearly visible in the longitudinal sections (Fig. 8).

Spicules. Styles to subtylostyles measuring 326-940 x 3.9-15 µm, and oxeas (sometimes with centrotylote) measuring 106-630 x 1-7.5 µm (Fig. 6 G, Fig. 9 C, D,

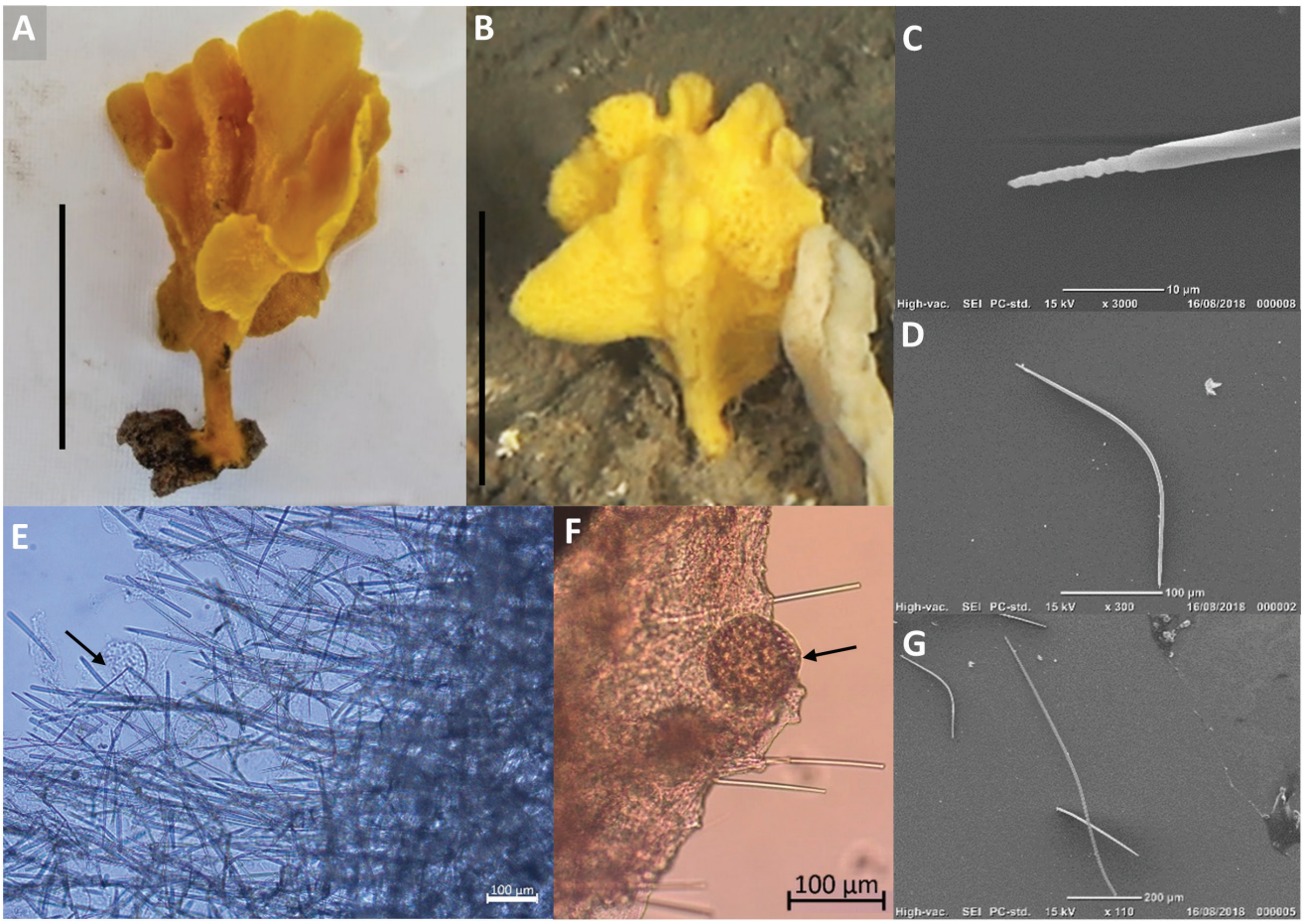

Fig. 6: *Axinella venusta* sp. nov. morphological characteristics. A. *A. venusta* sp. nov holotype; B. *A. venusta* sp. nov. *in situ* at the Atlit site, scale bar A, B 5 cm; C. Oxea with a stepped point; D. Curved oxea; E. Skeletal arrangement, large oocytes are visible (arrow); F. Spicules protruding the ectosome, large oocytes are visible (arrow); G. flexuous oxea.

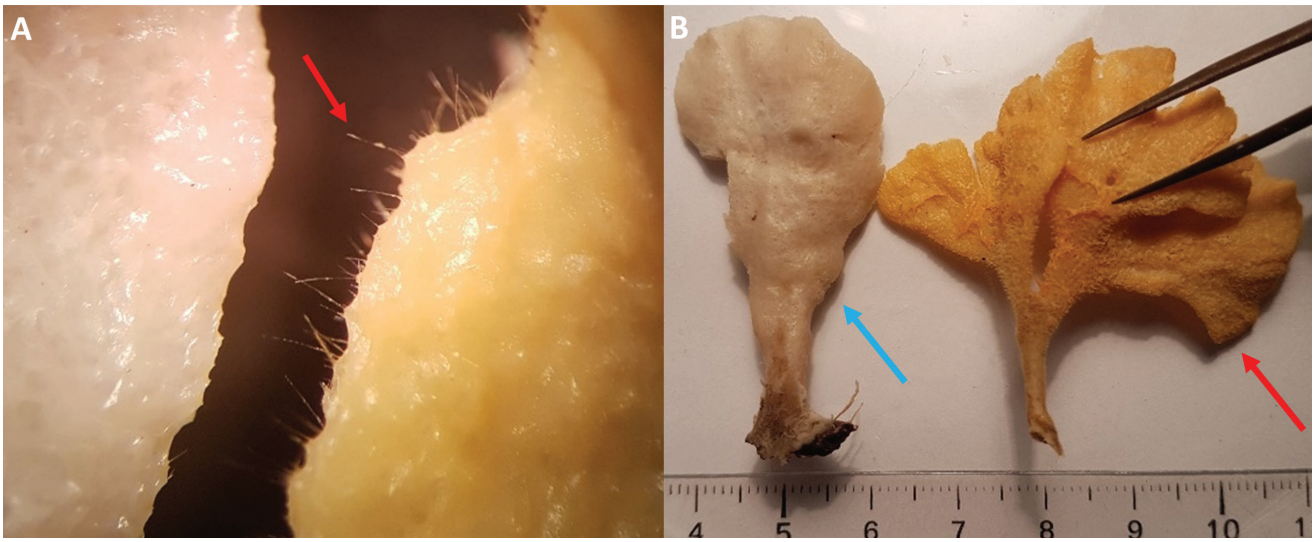

Fig. 7: *Axinella venusta* sp. nov. (paratype) and *A. vaceleti* side by side. A. close-up of the sponge surface, many protruding spicules are visible in *A. vaceleti* (arrow) while *A. venusta* sp. nov. (on the left) has only a few short protruding spicules; B. *A. venusta* sp. nov. (blue arrow) and *A. vaceleti* (red arrow).

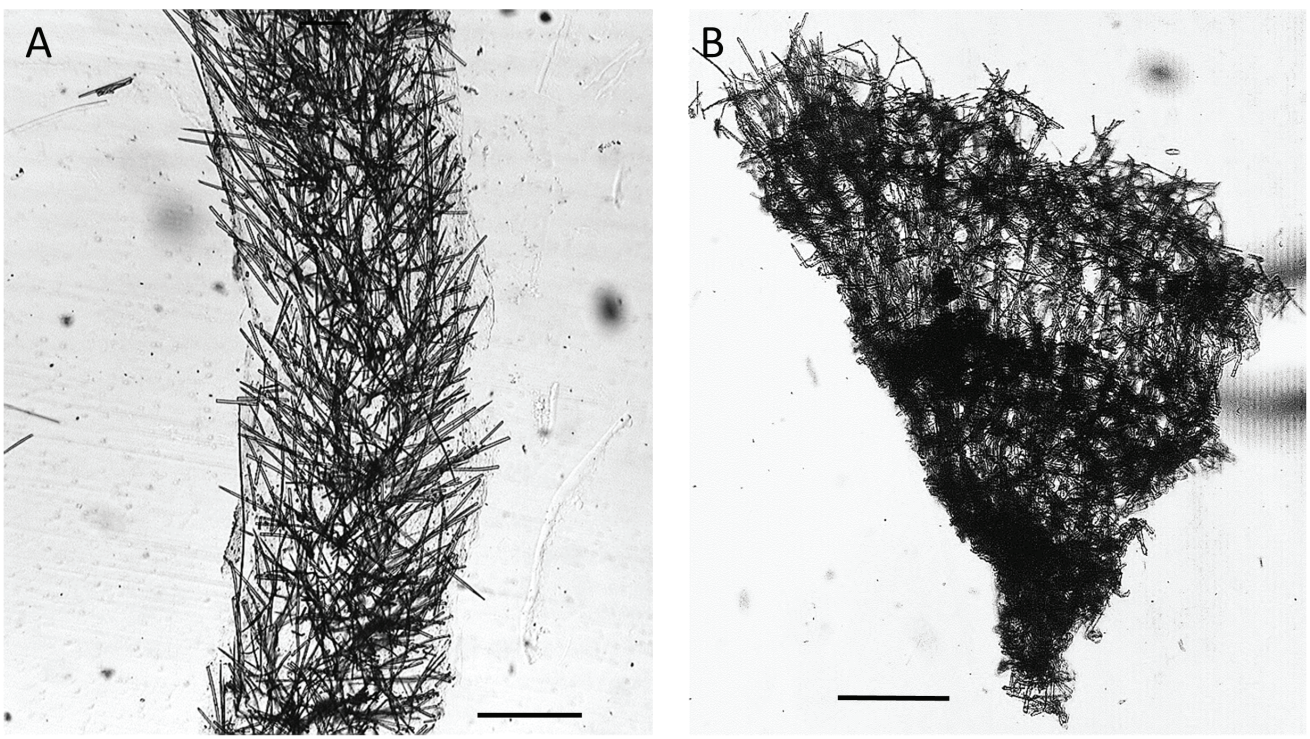

Fig. 8: Skeletal structure of *A. venusta*, scale 200 µm. A. longitudinal section of the narrow aspect; B. longitudinal section of the wide aspect.

G and Table 3). The oxeas are slightly curved to curved (Fig. 6 D, Fig. 9 A, B and Table 3), while the styles are slightly curved, curved, angulated or flexuous (Fig. 6 G Fig. 9 C, D, G and Table 3). The pointing end of the oxeas is regularly acerate or stepped (Fig. 6 C, Fig. 9 E, F).

Molecular. COI, 28S and 18S were already sequenced in our previous study, where *Axinella venusta* sp. nov. was referred to as *Axinella* sp.1 (Idan *et al.*, 2018). *A. venusta* 28S sequence was submitted to a BLAST search against Axinellidae sequences. Sequences that covered more than 50% of the *A. venusta* sequence were downloaded and aligned using MAFFT (Katoh *et al.*, 2005). Sequences AY864743 (*Ptilocaulis gracilis*) and MK372886 (*Epipolasis spissa*) were omitted from the alignment since they were different from the other Axinellidae sequences, as observed by eye. Positions that had more than 50% gaps were also deleted from the alignment. A maximum-likelihood phylogenetic tree was reconstructed with PhyML (Guindon *et al.*, 2010) using the GTR substitution model (Fig. S2). *A. venusta* grouped with *A. polypoides*, the type-species of the genus *Axinella* in phylogenetic analyses base on the COI, 18S (Fig. S1 and S2 in Idan *et al.*, 2018) and 28S (Fig. S2) sequences. Therefore, we concluded, at the time, that it was indeed

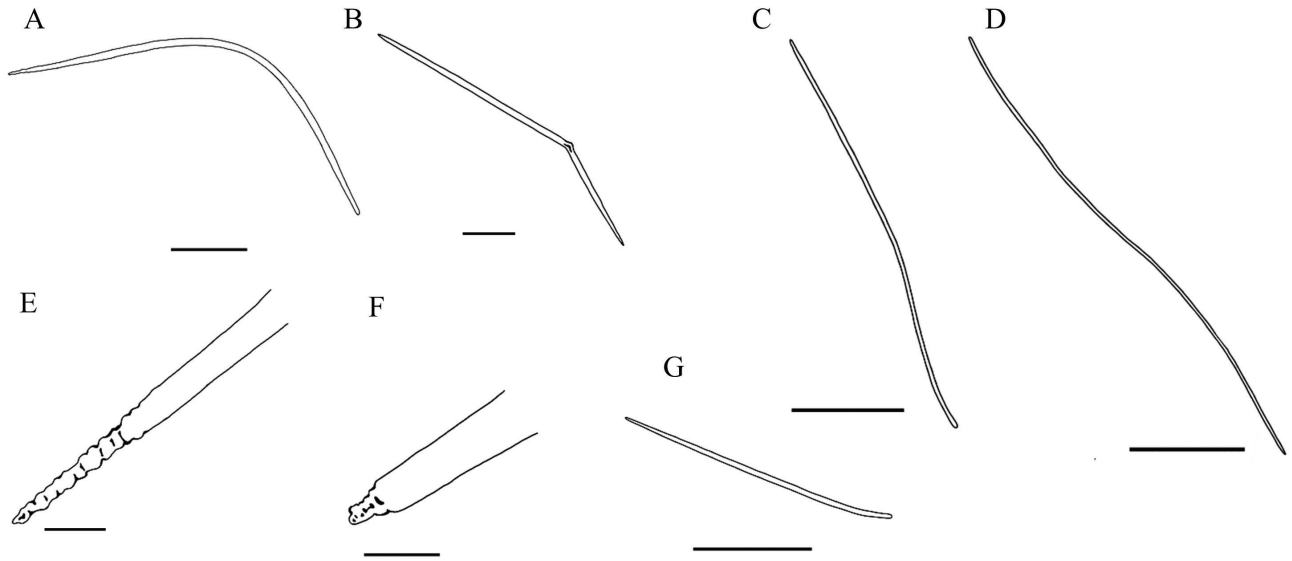

Fig. 9: Spicule of *Axinella venusta* sp. nov.: A. Oxea; B. Centrotylote oxea; C-D and G. Styles; E-F. Variations of stepped points of oxea. Scale bars: A-B, 50 µm; C-D, G 200 µm; E-F, 10 µm. Figure drawn by Michelle Dan.

Table 3. Comparison of morphological characteristics between *Axinella venusta* sp. nov. and morphologically or genetically related Mediterranean species.

	A. vaceleti* Pansini, 1984	***A. minuta* Lévi, 1957***	***A. pyramidata* Stephens, 1916***	***A. venusta* sp. nov. holotype**	***A. venusta* sp. nov. paratype**
Size	5-6 x 4-5 cm	2 x 0.2 cm	1.5 x 1.7 cm	10.5 cm x 4.5 cm	5 cm x 2.7 cm
Color	Orange	Not described	Pale brown, beige	Bright yellow-orange	Bright yellow-orange
Shape	Flabellate with small peduncle	Encrusting with a few perpendicular extensions	Three-sided pyramid standing on its apex	Foliaceous with small peduncle	Flabellate with small peduncle
Styles (µm)	270-1450 x 2.5-14 subtylostyles found	1200-1700 x 11-30 120-300 x 5.5-14	230-1000 x 10-16 subtylostyles found	326-940 x 3.9-15 subtylostyles found	153-1013 x 3-11.5 subtylostyles found
Oxea (µm)	250-370 x 2-12	260-400 x 6.5-13	300-600 x 10-16 centrotyloxea found	106-630 x 1-7.5 centrotyloxea found	150-375 x 3-10 centrotyloxea found

***** *A. vaceleti* (Pansini, 1984), *A. minuta* (Levi, 1957), *A. pyramidata* (Stephens, 1916).

an *Axinella* sp. following the revision of the *Axinella* genus by Gazave *et al.* (2010). The BLAST search revealed the 28S and 18S sequence of *A. pyramidata* are 98% (741/760 nucleotides, 0/760 gaps, E value 0.0) and 99.5% (1107/1109 nucleotides, 0/1109 gaps, E value 0.0) identical, respectively. 18S also shows 99% (1102/1109 nucleotides, 0/1109 gaps, E value 0.0) similarity to *A. vaceleti*, but for the 28S there is only 89% identical sequencing (684/767 nucleotides, 11/767 gaps, E value 0.0).

Distribution and ecology notes. Two specimens of *A. venusta* sp. nov. were collected from the mesophotic sponge grounds. While small in size (Fig. 6 A-B), this species is one of the six most common species in the Herzliya sponge ground (Idan *et al*., 2018 referred to as *Axinella* sp.1). It is also very common at the other studied mesophotic sites along the Israeli coast: Atlit, Rosh Carmel, and Shefayim.

Taxonomic remarks. The external morphology and spicule sizes of this sponge are ostensibly similar to those of *A. vaceleti* (Table 3, Fig. 6-9). However, when compared with both fresh and preserved specimens of the latter (kindly provided by Dr. Jean Vacelet and Dr. Thierry Pérez), several differences can be observed. The novel species is much stiffer than *A. vaceleti*, which is very soft and flexible; the thickness of the lamella of the novel species is 3-5 mm, while in *A. vaceleti* the maximal thickness of the lamella is 1.5 mm. Many long spicules protrude from the surface of *A. vaceleti*, giving it a velvety appearance; while *A. venusta* sp. nov. appears smooth and has only a few protruding spicules (Fig. 9). Moreover, the color of the novel species is a bright yellow-orange (Fig. 6), in contrast to *A. vaceleti*, which is dark orange (Pansini, 1984).

A. pyramidata, which is genetically the closest species to *A. venusta*, differs in both shape and color. *A. pyramidata* is much smaller than *A. venusta*, its shape is of an inverted three-sided pyramid, and its color is grey to off-white (Picton & Goodwin, 2007; Stephens, 1916).

Etymology. The species is named *venusta* in reference to its beauty and grace.

Class Homoscleromorpha Bergquist, 1978
Order Homosclerophorida Dendy, 1905
Family Plakinidae Schulze, 1880
Genus *Plakortis* Schulze, 1880
***Plakortis mesophotica* sp. nov.**

Material examined. Holotype – Po.25927, site: Herzliya, date: 28.07.15, ~100 m depth, collection site: 32.176250º N, 34.633056º E.

Description. Massive morphology, 3.5 x 3 x 1.5 cm. Color of live specimen is gray to tan (Fig. 10A). Surface smooth, with some irregular folds and grooves, mucoid, oscules 2-4 mm diameter (Fig. 10A, Table 4). Skeleton densely confused, with ectosomal specialization; spicules packed more densely in the ectosome but with no differential location (Fig. 11).

Skeleton. Densely confused skeleton, spicule density is highest in the ectosome (Fig. 11).

Spicules. Mostly diods centrotylote or with knobby-knotty centers, curved to somewhat sinuous, 48-100 x 2-5µm (Table 4, Fig. 9 B-C and 12 F-J). Triods 7.5-45 µm, some sagittal; the ends of the triod actines are acerate or blunt (Fig. 9 D and 12 A-E).

Molecular. COI gene was amplified and sequenced. GenBank accession number: COI KX866773. The closest species to *P. mesophotica*, with 97% similarity, is *Plakortis halichondrioides*, known from the eastern Caribbean (Moraes & Muricy, 2003). A phylogenetic tree including *P. mesophotica* (referred to as *Plakortis* sp.) and *P. simplex* described from the Israeli coast can be found in Idan *et al*. (2018).

Distribution and ecological notes. The specimen of *P. mesophotica* sp. nov. was not intentionally collected but found in the collection basket together with *A. damicornis*, *D. incisa*, *S. foetidus*, *C. sporadense*, *A.* and *H. verae*. Due to the small size of the species, we were not able to detect it in the images taken underwater, making it hard to assess its distribution. However, it has not been

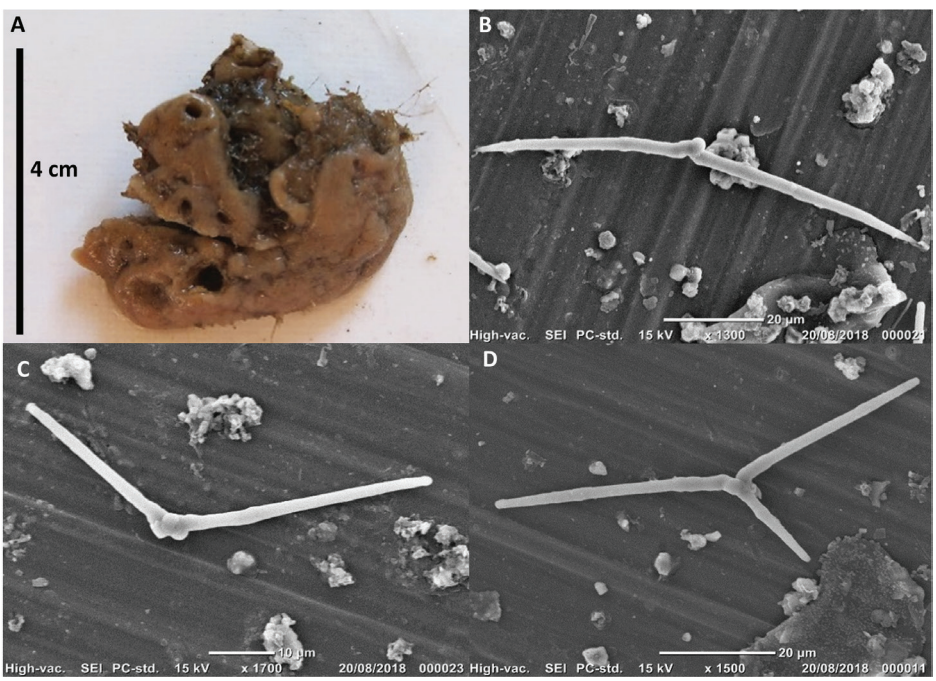

Fig. 10: *Plakortis mesophotica* sp. nov. morphological characteristics. A. *P. mesophotica* sp. nov. holotype; B-C. Diods can be straight or curved, smooth, acerate, with a central irregularity varying from very slightly to markedly S-shaped or centrotylote-like; D. Triods, irregular T-shaped and smooth.

Table 4. Comparison of morphological characteristics between *Plakortis mesophotica* sp. nov., *P. simplex* Schulze, 1880 and *P. halichondrioides* (Wilson, 1902).

	P. simplex* Schulze, 1880	***P. halichondrioides* (Wilson, 1902)***	***P. mesophotica* sp. nov.**
Size, shape and color	Thinly-encrusting sponges; generally 0.2-0.5 mm thick; white, yellow, light brown	Massively encrusting cake shaped; 5 x 1.5 cm; dark brown to black	Massively encrusting to massive; 4.7 x 4 cm; beige-gray
Diods (µm)	60-160 x 3-6	100-200 x 4-5	48-100 x 2-5
Triods (µm)	25-50 x 3-6	Not described (rare in later collected specimens)	7.5-45 x 1-9

***** *P. simplex* (Hooper & van Soest, 2002; Schulze, 1880), *P. halichondrioides* (Moraes & Muricy, 2003)

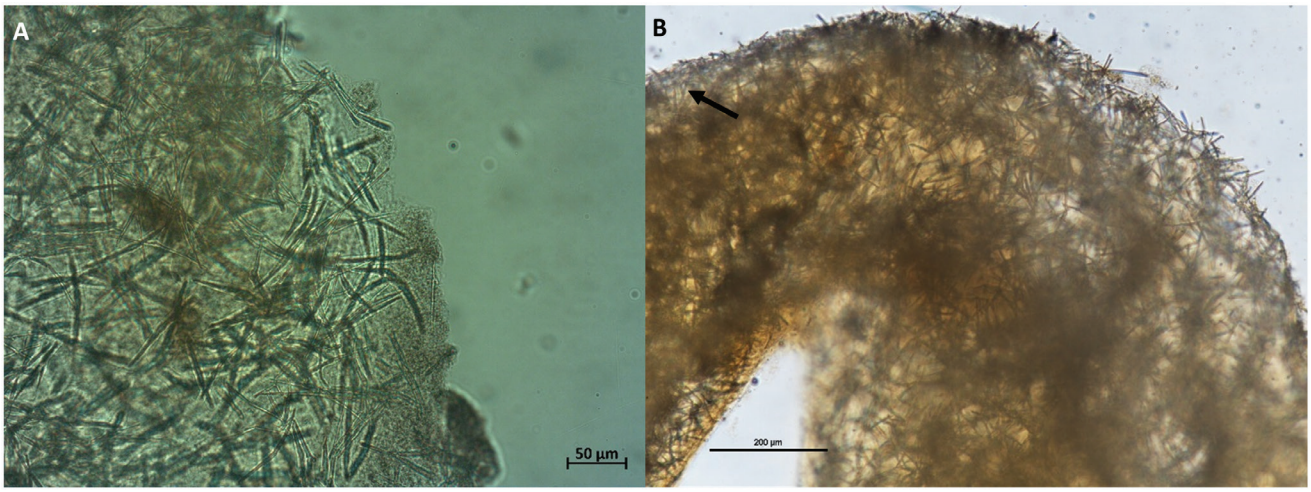

Fig. 11: *Plakortis mesophotica* sp. nov. skeletal arrangement. A. Diods scattered with no visible organization; B. Densely confused skeleton, spicule density is higher in the ectosome (black arrow).

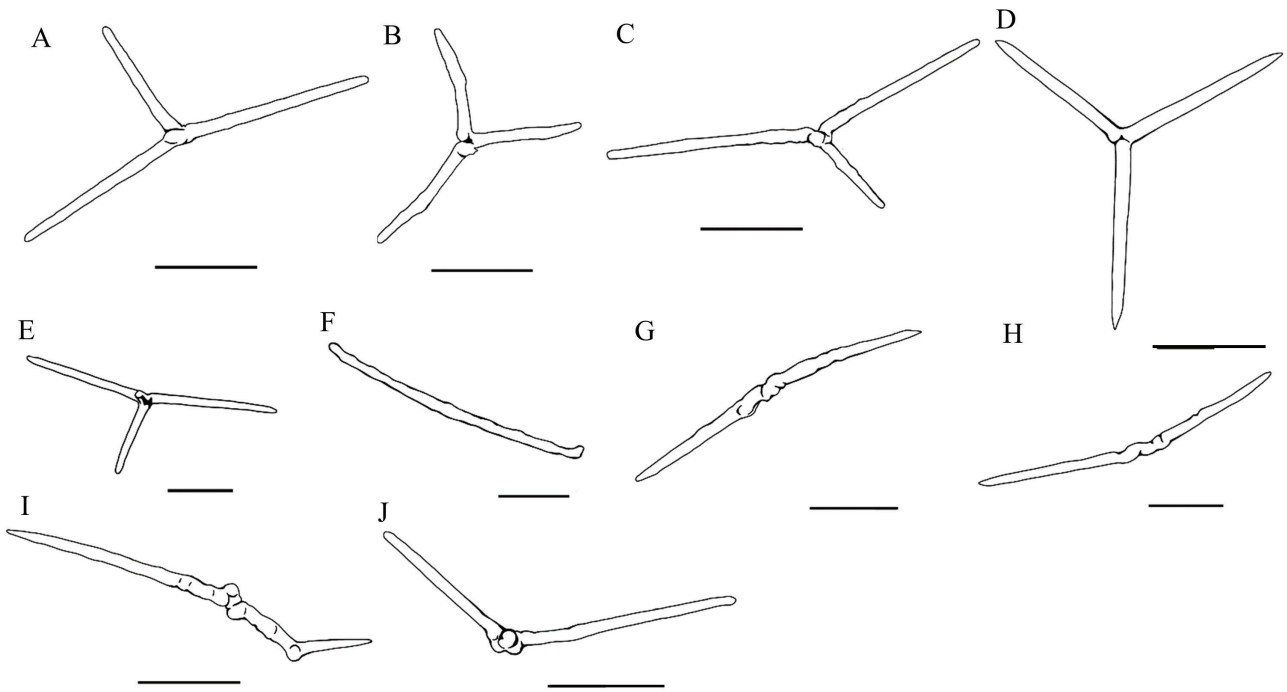

Fig. 12: Spicules of *Plakortis mesophotica* sp. nov., A-E. Triods; F-J. Diods. T-shaped triods (A, E), irregular (B) and smooth (D). Straight diods (F, G) or curved (H, J), smooth, acerate, with a central irregularity varying from very slightly (G, H) to markedly (J), S-shaped (I) or centrotylote-like (J). Scale bar 20 µm. Figure drawn by Michelle Dan.

detected in shallow water, unlike *P. simplex* reported by Tsurnamal (1968).

Taxonomic remarks. The only species of *Plakortis* known so far from the Mediterranean Sea, including the coast of Israel, is the cosmopolitan *P. simplex* Schulze, 1880 (van Soest *et al*., 2021). *P. mesophotica* sp. nov. does not fit the description of *P. simplex* neither in external morphology nor in spicule size (Table 4). While *P. simplex* is described as thinly-encrusting, *P. mesophotica* sp. nov. is massively encrusting to massive (Fig. 10 A). *P. simplex* usually has a lightish color: brown, white, yellow, or tan, and a surface described as smooth and regularly pierced by ostia (Hooper & van Soest, 2002; Schulze, 1880), while in *P. mesophotica* sp. nov. it is irregular with many folds and grooves. Spicules of *P. simplex* are somewhat smaller than those of *P. mesophotica* sp. nov. (Table 3; Hooper & van Soest, 2002; Schulze, 1880). Molecular analysis revealed only 96% similarity between *P. simplex* and *P. mesophotica* sp. nov. The species *P. halichondrioides*, which is molecularly the closest to *P. mesophotica* sp. nov. (similarity 97%), is very different in morphology, being described as dark brown to black. The diods are larger than in *P. mesophotica* sp. nov. (Table 4) and no triods were found in the holotype, although in later collected specimens of *P. halichondrioides* triods were rarely seen (Wilson, 1902; Moraes & Muricy, 2003).

Etymology. The species name *mesophotica* refers to the habitat in which it was found.

Updated checklist

Extensive surveys were carried out during 2016-2019 in the mesophotic zone of the Israeli Mediterranean coast. Over 100 specimens were collected and classified to the lowest possible taxonomic level. These surveys, together with the collection carried out by Idan *et al*. (2018) have resulted in the addition of 33 species to the local species list (Table 5), elevating the local richness by ~34% (Idan *et al*., 2018). The current update adds seven more species to those of the Israeli coast: *Axinella vaceleti*, *Axinella* sp.3, *Axinella* sp.4, *Spongia (Spongia) lamella*, Haplosclerida sp.1, *Haliclona poecillastroides* and *Corticium candelabrum*. Moreover, *Petrosia (Petrosia) ficiformis* and *Aaptos aaptos*, that are known from the shallow water of the Israeli coast were also found in the mesophotic sponge grounds. The current checklist also provides the distribution of the identified species at seven mesophotic sites along the coast.

Table 5. Updated checklist of sponge species collected from the mesophotic sponge ground and their distribution at the mesophotic sites, along the shallow Israeli coast, and in the Levantine Sea. * reported in Tsurnamal (1968). ? unknown distribution of species that are not yet identified. [a] Jean Vacelet, personal communication, identified from photo. [b] Thierry Pérez, personal communication. HR = Herzliya, AT = Atlit, RC = Rosh Carmel, HD = Hadera, SH = Shefayim, TA = Tel Aviv. Sites coordinates and characteristics are provided in Table 1.

	Lowest systematic identification level	Museum #	Site	Family	Order	Upper-photic zone Israel	Levant Basin
Demospongiae							
1	*Agelas oroides* (Schmidt, 1864)*	25669; 25598	HR, AT, RC, HD, SH, TA	Agelasidae	Agelasida	-	+
2	*Axinella damicornis* (Esper, 1794)	25764	HR, AT, RC, SH	Axinellidae	Axinellida	-	-
3	*Axinella polypoides* Schmidt, 1862	25597	HR, AT, RC, HD, SH	Axinellidae	Axinellida	+	+
4	*Axinella venusta* sp. nov.	25779; 26035	HR, AT, RC, HD, SH	Axinellidae	Axinellida	-	-
5	*Axinella vaceleti* Pansini, 1984	26438	HR, SH, RC, AT	Axinellidae	Axinellida	-	-
6	*Axinella verrucosa* (Esper, 1794)	25668; 25674	HR, AT, RC, HD, SH	Axinellidae	Axinellida	+	+
7	*Axinella* sp.2	25781	HR, AT, RC	Axinellidae	Axinellida	-	?
8	*Axinella* sp.3	26259	AT	Axinellidae	Axinellida	-	?
9	*Axinella* sp.4	26437	RC	Axinellidae	Axinellida	-	?
10	*Raspailia (Raspailia) viminalis* Schmidt, 1862*	25743	HR, AT, RC, SH	Raspailiidae	Axinellida	-	+
11	*Dictyonella incisa* (Schmidt, 1880)	25741; 25919	HR, AT, RC, SH, HD, TA	Dictyonellidae	Bubarida	-	-
12	*Dictyonella* sp.1	25926	RC	Dictyonellidae	Bubarida	-	?
13	*Thymosiopsis conglomerans* Vacelet, Borchiellini, Perez, Bultel-Poncé, Brouard & Guyot, 2000	25914	HR, AT, RC, HD, SH	Chondrillidae	Chondrillida	-	-
14	*Chondrosia reniformis* Nardo, 1847*	25664; 25776; 25930	NA, HR, SH, TA, AT, RC	Chondrosiidae	Chondrosiida	+	+
15	*Lamellodysidea* sp.1	25778	HR	Dysideidae	Dictyoceratida	-	?
16	*Ircinia dendroides* (Schmidt, 1862)	25830; 25831	HR, AT, RC,	Irciniidae	Dictyoceratida	+	+
17	*Ircinia oros* (Schmidt, 1864)	25670	HR, AT, RC, HD, SH	Irciniidae	Dictyoceratida	-	+

Continued

Table 5 continued

	Lowest systematic identification level	Museum #	Site	Family	Order	Upper-photic zone Israel	Levant Basin
18	*Ircinia variabilis* (Schmidt, 1862)*	25918; 25492	HR, AT, RC, SH	Irciniidae	Dictyoceratida	+	+
19	*Sarcotragus foetidus* Schmidt, 1862*	25921	HR, AT, RC, SH, TA	Irciniidae	Dictyoceratida	+	+
20	*Sarcotragus spinosulus* Schmidt, 1862*	25673; 25666	HR, AT, RC, HD	Irciniidae	Dictyoceratida	+	+
21	*Spongia (Spongia) nitens* (Schmidt, 1862)	25742; 25493	HR, AT, RC	Spongiidae	Dictyoceratida	-	-
22	*Spongia (Spongia) zimocca* Schmidt, 1862	25742	HR	Spongiidae	Dictyoceratida	-	+
23	*Spongia (Spongia) lamella* (Schulze, 1879)	26215	HR, SH	Spongiidae	Dictyoceratidae	-	+
24	*Coscinoderma sporadense* Voultsiadou-Koukouras, van Soest & Koukouras, 1991	25932	HR, RC, SH, AT	Spongiidae	Dictyoceratida	-	-
25	*Fasciospongia cavernosa* (Schmidt, 1862)	26241	HR, RC, HD, SH	Thorectidae	Dictyoceratida	+	+
26	Dictyoceratida sp.1	25766	HR	?	Dictyoceratida	-	?
27	Haplosclerida sp.1	26280	HR	?	Haplosclerida	-	?
28	Chalinidae sp.1	25928	HR	Chalinidae	Haplosclerida	-	?
29	*Chalinula* sp.1	25782	HR	Chalinidae	Haplosclerida	-	?
30	*Haliclona poecillastroides* (Vacelet, 1969)[a]		RC	Chalinidae	Haplosclerida	-	-
31	*Haliclona* sp.1	25929	HR	Chalinidae	Haplosclerida	-	?
32	*Petrosia (Petrosia) ficiformis* (Poiret, 1789)	26243	HR, RC, SH	Petrosiidae	Haplosclerida	+	+
33	*Calyx nicaeensis* (Risso, 1826)	25570	HR, AT, RC, SH	Phloeodictyidae	Haplosclerida	-	+
34	*Phorbas tenacior* (Topsent, 1925)	26398	HR, RC, SH	Hymedesmiidae	Poecilosclerida	-	+
35	*Phorbas topsenti* Vacelet & Pérez, 2008	25767	NA, HR, SH, TA, AT, RC	Hymedesmiidae	Poecilosclerida	+	+
36	*Aaptos aaptos* (Schmidt, 1864)*	26082	RC, HR, SH	Suberitidae	Suberitida	+	+
37	*Hemiasterella verae* sp. nov.	25931	HR	Ancorinidae	Tetractinellida	-	-
38	*Stryphnus mucronatus* (Schmidt, 1868)	25733	HR, AT, RC, SH	Ancorinidae	Tetractinellida	-	-
39	*Aplysina cavernicola* (Vacelet, 1959)	25922; 25923	HR, AT, RC, SH	Aplysinidae	Verongiida	-	-
Homoscleromorpha							
40	*Oscarella lobularis* (Schmidt, 1862)*[b]	25935	HR, AT, RC, SH	Oscarellidae	Homosclerophorida	+	+
41	*Oscarella tuberculata* (Schmidt, 1868)[b]	25934	HR, AT, RC, SH	Oscarellidae	Homosclerophorida	-	-
42	*Oscarella* sp.1	25936	HR	Oscarellidae	Homosclerophorida	-	?
43	*Corticium candelabrum* Schmidt, 1862	26254	HR, RC, SH, AT	Plakinidae	Homosclerophorida	-	+
44	*Plakortis mesophotica* sp. nov.	25927	HR	Plakinidae	Homosclerophorida	-	-

Concluding remarks

The discovery of three new species in the Israeli mesophotic zone is not surprising. Results from the latest expeditions have shown that the rocky substrates of the Israeli mesophotic zone are characterized by unexpectedly high sponge richness and substantial diversity, hosting at least 40% of the known Israeli sponge fauna (Table 5 and Table S1 in Idan *et al*., 2018). However, these surveys are still far from being complete, since many of the species found in the mesophotic sponge grounds are small, inconspicuous, and difficult to sample, or even to quantify their abundance. *Plakortis mesophotica* sp. nov. and *Hemiasterella verae* sp. nov, both belong to this group. *Axinella venusta* sp. nov., in contrast, is highly abundant in all study sites (Table 5). The discovery of these species (as well as several others that still await description; Table 5) emphasizes the importance of studying ecosystems and habitats that are not easily accessible. Such studies are bound to yield additional discoveries of novel species. Further research of the sponges comprising the benthic assemblages of the mesophotic habitats is needed, both in order to establish a baseline of data regarding the fauna there, and also in support of conservation attempts for these unique habitats. In Israel, in the last couple of years, a great effort has been invested in establishing near-shore marine reserves. A greater challenge still lies in the establishment of deeper-water marine reserves, which, due to their distance from shore, makes them harder to promote among the public and policymakers. Consequently, it is easier to convey the importance of preserving such habitats when they feature unique, novel, and endemic species.

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Supplementary data

The following supplementary information is available online for the article:

Fig. S1: Phylogenetic tree used to support the morphological identification *Hemiasterella verae* sp. nov. (marked by '*'). The maximum likelihood tree was reconstructed with PhyML 3.0 (Guindon *et al*., 2010) based on 28S rDNA sequences, using the GTR model of sequence evolution. Bootstrap supports are given near the corresponding nodes.

Fig. S2: Phylogenetic tree based on 28S rDNA sequences, used to support the morphological identification of *Axinella venusta* sp. nov. (marked by '*'). The maximum likelihood tree was reconstructed with PhyML 3.0 (Guindon *et al*., 2010), using the GTR model of sequence evolution. Bootstrap supports (100 replicates) given near the corresponding nodes.