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Taxonomic composition and assemblage structure of brachiopods from two submarine caves in the Aegean Sea, Eastern Mediterranean

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Abstract

Brachiopods exhibit a particular preference for cryptic habitats such as submarine caves. However, their assemblages have rarely been investigated quantitatively in this habitat. In this work, brachiopod assemblages were studied in detail for the first time in two Aegean submarine caves, Fara and Agios Vasilios, Lesvos Island, Eastern Mediterranean Sea. Six species of Recent brachiopods, i.e. *Novocrania turbinata* (Poli, 1795), *Tethyrhynchia mediterranea* Logan, 1994, *Megathiris detruncata* (Gmelin, 1791), *Argyrotheca cuneata* (Risso, 1826), *A. cistellula* (Searles–Wood, 1841), and *Joania cordata* (Risso, 1826), have been identified. The cave-exclusive species *Tethyrhynchia mediterranea* is reported for the first time from the Aegean Sea and Greek waters, increasing the regional brachiopod fauna to 13 species, and for the second time in the Eastern Mediterranean. Five species were present in both caves while *T. mediterranea* was found only in the internal dark ceilings and walls of Fara cave. In both caves the dominant species was *Argyrotheca cuneata*. Abundance and diversity increased towards the internal dark ceilings of both caves, which harboured a well-differentiated brachiopod assemblage compared to that of the outer cave zones.

Keywords: *Brachiopoda, submarine caves, biodiversity, Aegean Sea, Eastern Mediterranean*

Introduction

Brachiopods are sessile, marine invertebrates with a long geological history. Today, represented by approximately 400 species (Emig et al. 2013), brachiopods are considered a minor phylum, however, they are widely distributed geographically, living in all oceans. The shallow-water micromorphic species are commonly found in shaded, light-poor environments, such as cryptic and cave habitats where they can occur in high densities. Mediterranean marine caves constitute important hot-spots for brachiopod diversity, harbouring 10 (70%) out of the 14 species occurring in the Mediterranean Sea (Gerovasileiou & Bianchi 2021). Although brachiopods have been reported from many submarine caves (e.g. Logan 1979, 2003; Monteiro-Marques 1981; Logan & Noble 1983; Logan & Zibrowius 1994; Simon & Willems 1999; Boury-Esnault et al. 2001; Logan et al. 2002, 2004; Harmelin et al. 2003; Rosso et al. 2013; Gerovasileiou et al. 2015; Radolović et al. 2015; Sanfilippo et al. 2015;

Guido et al. 2017; Simon et al. 2018; Jimenez et al. 2019), their assemblage structure has rarely been investigated in detail. Existing quantitative studies have focused on particular species, but never in the Eastern Mediterranean Sea. Taddei Ruggiero (1994, 1996, 2001) carried out studies on the population of *Novocrania anomala* (Müller, 1776) from Isca cave, Tyrrhenian Sea, Italy. Logan (2001) conducted a morphometric analysis of the populations of *Megathiris detruncata* (Gmelin, 1791) from caves in the Western Mediterranean and Northeastern Atlantic. Recently Bergamin et al. (2020) studied the composition and distribution patterns of the dead brachiopod assemblage found in cave sediment of the CT12 cave in southern Spain.

Here we present the first quantitative study of brachiopod biodiversity, assemblage structure and spatial variability in two submarine caves of the Aegean Sea, Eastern Mediterranean (Figure 1). The main goals of the study were to increase knowledge on the regional

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cave species diversity but also to provide a better understanding of the spatial variability of brachiopod assemblages in this peculiar habitat.

Material and methods

Study sites

Two marine caves were studied in Lesvos Island, Northeastern Aegean Sea (Eastern Mediterranean). The caves are located in the rock islets Fara and Agios Vasilios, off the southeastern coast of the island, hereafter indicated as F and AV, respectively (Figure 1). The F cave (38.969° N, 26.477° E; 14–18 m depth) is 32-m-long, ending in a dark chamber, connected through narrow fissures to a second chamber on the other side of the islet. The AV cave (38.969°N, 26.541°E; 24–40 m depth) is a funnel-shaped blind cave with a large entrance (16 m high x 7 m wide). In this study only the first 25 m part of the cave was surveyed, because beyond this distance, an ascending narrow and dark tunnel makes underwater work practically impossible. Both caves have been thoroughly

studied regarding their morphology (Gerovasileiou et al. 2013) and sessile benthic assemblages (Gerovasileiou et al. 2017; Guido et al. 2019a, 2019b), including detailed studies on sponges (Gerovasileiou & Voultsiadou 2016), serpulids (Sanfilippo et al. 2017) and bryozoans (Rosso et al. 2019), but this is the first study focusing on their brachiopod fauna.

Sampling process and sample analysis

Three replicate quadrats of 400 cm² (20 × 20 cm) were scraped from 10 sampling stations (6 in F cave and 4 in AV cave), in the summer 2010, by SCUBA diving. Sampling stations represented different assemblages of the sidewalls and ceiling, at different distances from the entrance of the caves (Table I). A total of 30 samples were collected (18 from F cave and 12 from AV cave) and preserved in 10% formalin. After the sorting process, all brachiopods were collected and identified. For the calculation of abundance, the number of complete individuals was added to the highest number of either ventral or dorsal valves (see Schröder et al. 2019). The

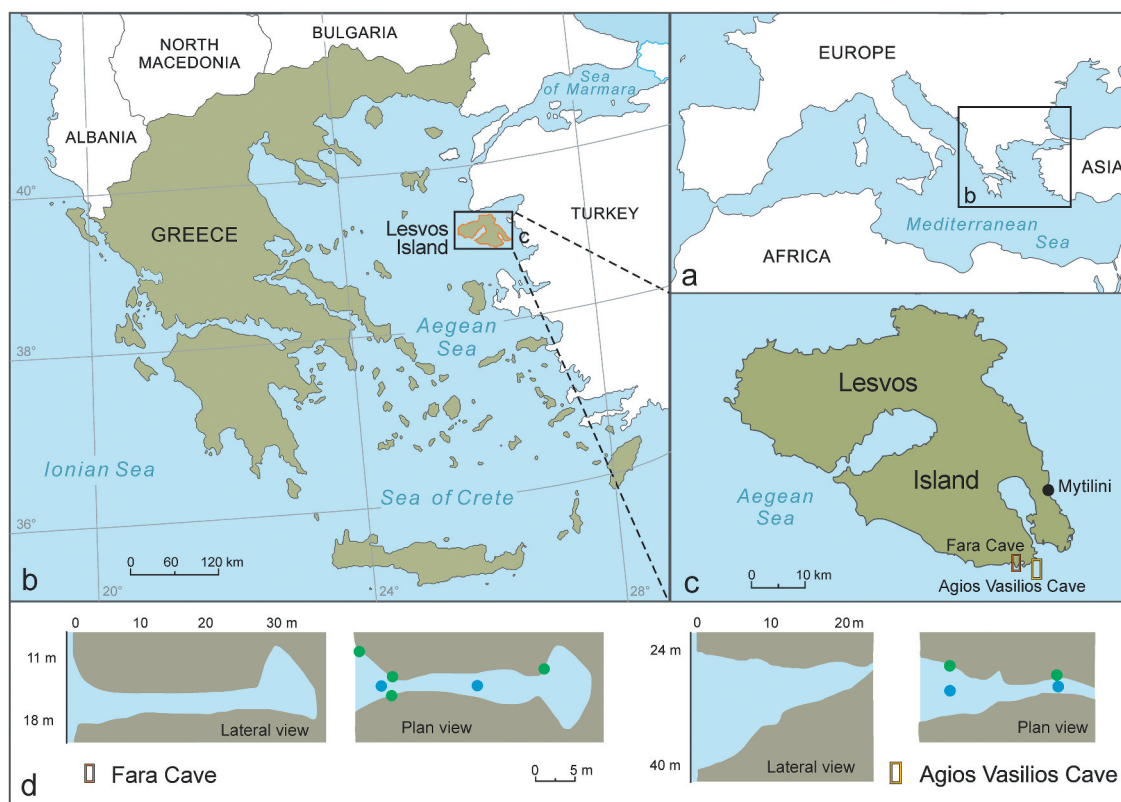


Figure 1. (a–c) Location of the studied caves in Lesvos Island, Aegean Sea, Eastern Mediterranean. (d) Lateral and plan views of the caves with indication of depth and location of collected samples in relation to distance from the entrances; blue circles: ceiling samples; green circles: wall samples.

Table I. Brachiopods recorded in the Fara and Agios Vasilios caves. The total number of individuals per sampling station is presented. For each sampling station the location inside the cave (L w, Left wall; R w, Right wall; C, Ceiling; and Entr, Entrance), distance from the entrance (m), biocoenosis (Cor, Coralligenous Biocoenosis; SD, Semidark Cave Biocoenosis; Trans, Transitional Zone; and Dark, Dark Cave Biocoenosis) and main sessile encrusters (Rh, Rhodophytes, Sc, Scleractinian corals; Sp, Sponges; Sr, Serpulid polychaetes; and B, Bryozoans) are indicated.

Cave	Fara Cave						Agios Vasilios Cave				
Depth (m)	11–18						24–40				
Sample location	L w	C	L w	R w	C	Walls	C	Walls	C	Walls	
Distance from entrance (m)	Entr	5	5–10	5–10	15–20	20–30	5–10	5–10	15–20	15–20	
Biocoenosis	Cor	SD	SD	SD	Trans	Dark	SD	SD	Dark	Dark	
Dominant encrusters	Rh	Sc-Sp	Sp	Sc-Sp	Sr-B	Sr-Sp-B	Sc-Sp	Sp	Sc-Sp-Sr	Sp-Sr	
Sampling stations/Brachiopoda	F1	FC1	F2	F3	FC2	F4	VC1	V1	VC2	V2	
<i>Novocrania turbinata</i> (Poli, 1795)		2			27	12	3		26	2	
<i>Tethyrhynchia mediterranea</i> Logan, 1994					2	1					
<i>Megathiris detruncata</i> (Gmelin, 1791)	2	2		1	66	27	12	2	66	21	
<i>Argyrotheca cuneata</i> (Risso, 1826)	7	9	3	2	256	40	41	20	231	17	
<i>Argyrotheca cistellula</i> (Searles-Wood, 1841)					3	6			6		
<i>Joania cordata</i> (Risso, 1826)	46	9	76	3	6	7	43	61	1	19	
Total number of individuals in all replicates	55	22	79	6	360	93	99	83	330	59	

total number of specimens is 1186 (615 in F cave and 571 in AV cave).

To remove soft tissue, specimens were treated with hypochlorite bleach, followed by a water wash. For scanning electron microscope (SEM) examination, the selected specimens were dried, mounted on stubs, coated with platinum, and examined using a Philips XL-20 microscope at the SEM laboratory of the Institute of Paleobiology, Warszawa. The investigated specimens are housed at the Hellenic Centre for Marine Research, Heraklion, Crete and in the collection of the Institute of Paleobiology, Warszawa under the catalogue number ZPAL Bp.85.

Data analysis

For each station, the brachiopod abundance (N), species richness (S), Shannon–Wiener diversity index (H'), Simpson's diversity index ($1-\lambda'$) and species evenness (J') were calculated. One-way permutational ANOVA (PERMANOVA) was used to examine the variability of the above measures across the stations of each cave (factor, Station; fixed with six levels for F cave and four levels for AV cave). The multivariate resemblance of sampling stations was investigated with cluster analysis, based on the Bray–Curtis similarity index (square root-transformed mean abundance) and using the SIMPROF (similarity profile) test to examine the null hypothesis of no meaningful structure within samples (significant differences at 5% level). The contribution of species to the Bray–Curtis similarity of samples within the resulting groups was estimated with SIMPER (similarity percentages). Statistical analysis

was undertaken using the PRIMER-E v.6 software package (Clarke & Gorley 2006).

Results

Taxonomic composition

Six brachiopod species belonging to five genera have been identified in the material collected in the two Aegean submarine caves, Fara and Agios Vasilios (Table I). Inarticulate and rhynchonellide brachiopods have one representative each, *Novocrania turbinata* (Poli, 1795) and *Tethyrhynchia mediterranea* Logan, 1994, respectively. The remaining four species, *Megathiris detruncata* (Gmelin, 1791), *Argyrotheca cuneata* (Risso, 1826), *A. cistellula* (Searles-Wood, 1841) and *Joania cordata* (Risso, 1826) are representatives of the family Megathyrididae. Two species, *Argyrotheca cuneata* and *Joania cordata* dominate in the studied material (52.8% and 22.8% of the total brachiopod specimens, respectively), followed by *Megathiris detruncata* (16.8%), *Novocrania turbinata* (6.1%), *Argyrotheca cistellula* (1.3%) and *Tethyrhynchia mediterranea* (0.2%) (Table I). The latter was found only in the F cave while the other five species were present in both caves.

Novocrania turbinata (Poli, 1795) is a cementing inarticulate brachiopod (Figure 2(a–d)), commonly found attached to hard substrates in shallow-water cryptic habitats, including walls or ceilings of caves (Logan & Long 2001; Logan et al. 2004). In the studied material it is present in both caves, being relatively common (see Table I). Initially, those brachiopods were assigned to *Novocrania anomala* (O.F.

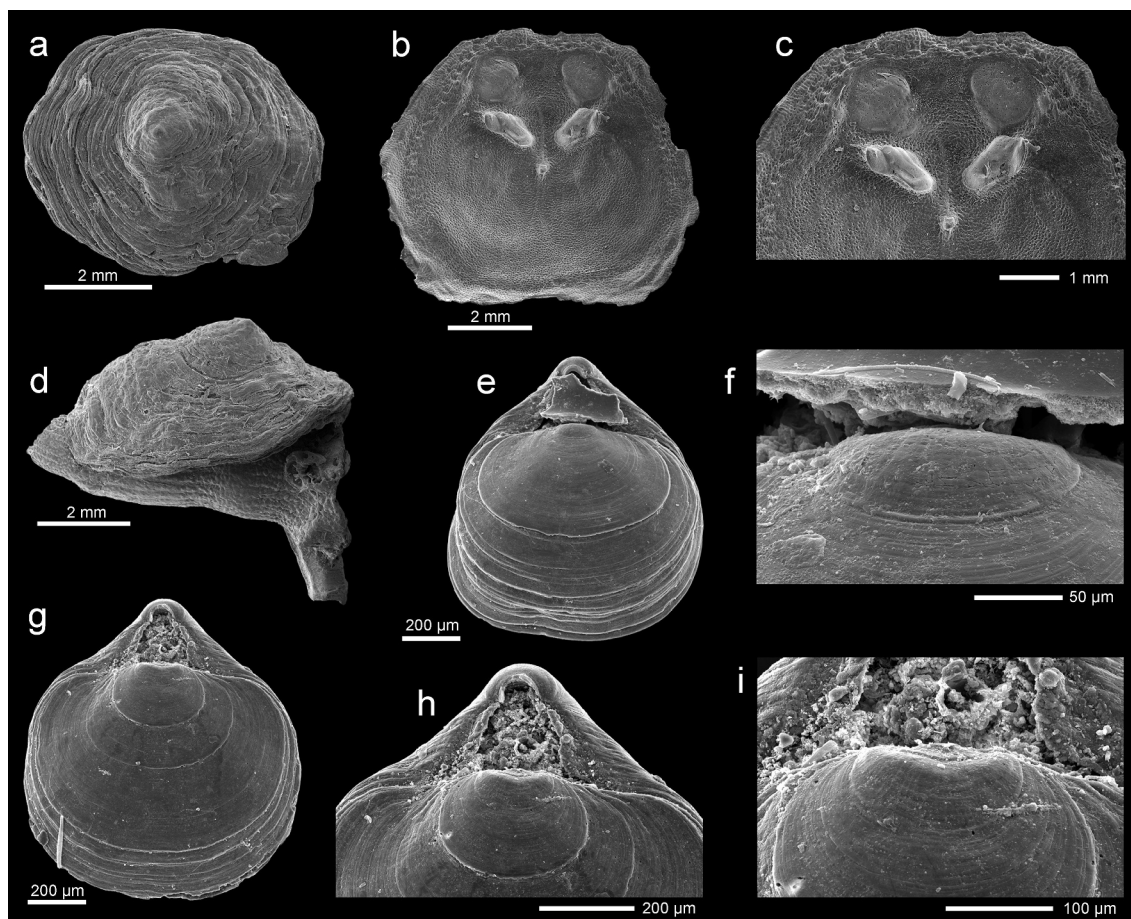


Figure 2. (a–d) *Novocrania turbinata* (Poli, 1795): (a) external outer view of dorsal valve, station FC2, ZPAL Bp.85/1; (b–c) inner view of dorsal valve and enlargement of posterior part to show details muscle scars, station FC2, ZPAL Bp.85/2; (d) lateral view of complete specimen, station VC2, ZPAL Bp.85/3. (e–i) *Tethyrhynchia mediterranea* Logan, in Logan & Zibrowius, 1994: (e–f) dorsal view of complete specimen and enlargement of umbonal part to show fine capillation anterior to the protegular node, station FC2, ZPAL Bp.85/4; (g–i) dorsal view of complete specimen, and enlargements of the umbonal part to show details of the beak and fine capillation anterior to the protegular node, station F4, ZPAL Bp.85/5. All SEM photos.

Müller, 1776) by Gerovasileiou et al. (2015, 2017) and Rosso et al. (2019). However, the examination of all specimens collected in the two caves of Lesvos Island revealed a thick ventral valve, thus corroborating attribution to *N. turbinata* according to Robinson (2017).

Tethyrhynchia mediterranea Logan in Logan & Zibrowius, 1994 is a diminutive rhynchonellide species, hardly exceeding 1 mm. It is characterized by the smooth surface with numerous growth lines, rectimarginate anterior commissure and high beak with a large, subtriangular, hypothyril foramen (Figure 2(e–i)). In the material under study, this species is very rare (three specimens), found only in F cave (Table I). *Tethyrhynchia mediterranea* can be considered as a cave-exclusive species and is likely to be endemic to the Mediterranean Sea (Logan et al. 2004).

Megathiris detruncata (Gmelin, 1791), a representative of the family Megathyrididae, is one of the most common species in both caves. It is common throughout the Mediterranean and Northeastern Atlantic (Logan 1979, 1993, 2003; Harmelin et al. 2003; Gerovasileiou et al. 2015; Sanfilippo et al. 2015; Gerovasileiou & Bailly 2016; Bergamin et al. 2020). It is characterized by the broadly transverse shell ornamented by rounded ribs (Figure 3(a–d)). The presence of three septa in the dorsal valve (Figure 3(e)) makes this species easily distinguishable from other members of Megathyrididae.

Argyrotheca cuneata (Risso, 1826) is the commonest species in the investigated material, present in both caves. This species is easily recognized by distinctive pink-red colouration between broad ribs. Its shell is variable from transversely elongate to subrectangular (Figure 3(f–i)). It is widely distributed throughout the

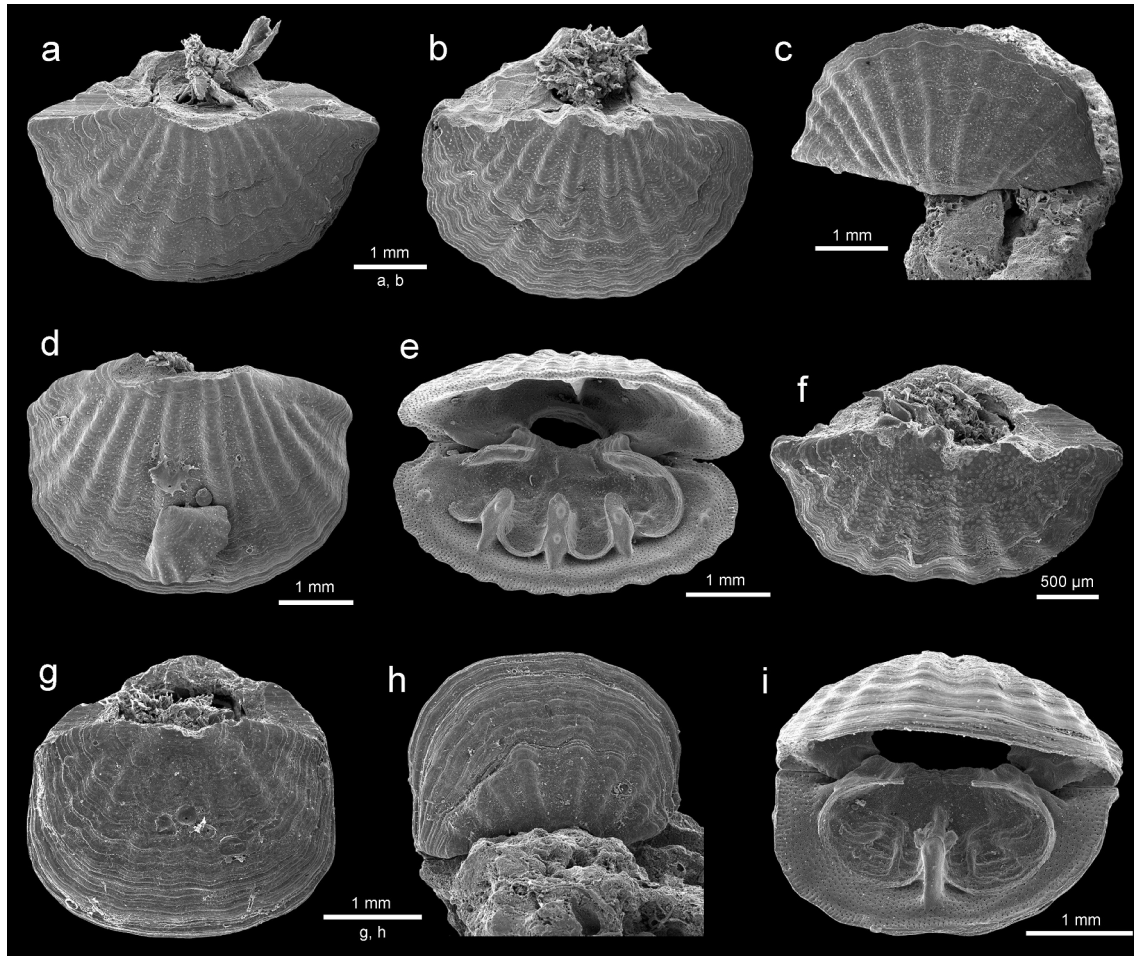


Figure 3. (a–e) *Megathiris detruncata* (Gmelin, 1791): (a–b) dorsal views of complete specimens, station FC2, ZPAL Bp.85/6–7; (c) complete specimen in living position attached to a bryozoan, station VC2, ZPAL Bp.85/8; (d) ventral view of complete specimen with attached immature specimen, station FC2, ZPALBp.85/9; (e) interior view to show three dorsal septa and brachidium, station VC2, ZPAL Bp.85/10. (f–i) *Argyrotheca cuneata* (Risso, 1826): (f–g) dorsal views of complete specimens, station FC2, ZPAL Bp.85/11–12; (h) complete specimen in living position, station VC2, ZPAL Bp.85/13; (i) interior view to show dorsal medium septum, brachidium and two rudimentary ascending branches diverging from the septum, station V2, ZPAL Bp.85/14. All SEM photos.

Mediterranean, being typical of the infralittoral-circalittoral zone (Logan 1979, 2003; Logan et al. 2004) but is also commonly found in caves (Taddei Ruggiero 1994, 1996; Grobe & Lüter 1999; Rosso et al. 2013; Gerovasileiou et al. 2015; Sanfilippo et al. 2015; Guido et al. 2017; Jimenez et al. 2019; Bergamin et al. 2020). *Argyrotheca cuneata* is also reported from the Northeastern Atlantic (Logan 1993).

Argyrotheca cistellula (Searles–Wood, 1841) has been found in both caves but it is very rare in the collected material (Table I). Its shell is extremely small, not exceeding 1.4 mm in width, squarely transverse in outline, smooth except numerous growth lines, and strongly biconvex (Figure 4(a–d)). This species is usually found in shallow water, commonly occurring in caves (Logan 1979; Logan 2001, 2003; Grobe & Lüter 1999; Simon & Willems 1999;

Harmelin et al. 2003; Logan et al. 2004; Rosso et al. 2013; Gerovasileiou et al. 2015; Bergamin et al. 2020). It is also noted from the Northeastern Atlantic (Logan 1993).

Joania cordata (Risso, 1826) is the second most common species in both caves. It is characterized by an elongate heart-shaped outline, semi-transparent shell with weakly defined ribs (Figure 4(e–h)). Internally it is easily distinguishable from other megathyridid species described here by the presence of tubercles on the inner margins of both valves. This species is very common in the Mediterranean, occupying the infralittoral-circalittoral zone and often found attached to cave walls and ceilings (Logan 1979, 2003; Taddei Ruggiero 1996, 2001; Grobe & Lüter 1999; Logan et al. 2004; Rosso et al. 2013; Gerovasileiou et al. 2015; Sanfilippo et al. 2015; Bergamin et al.

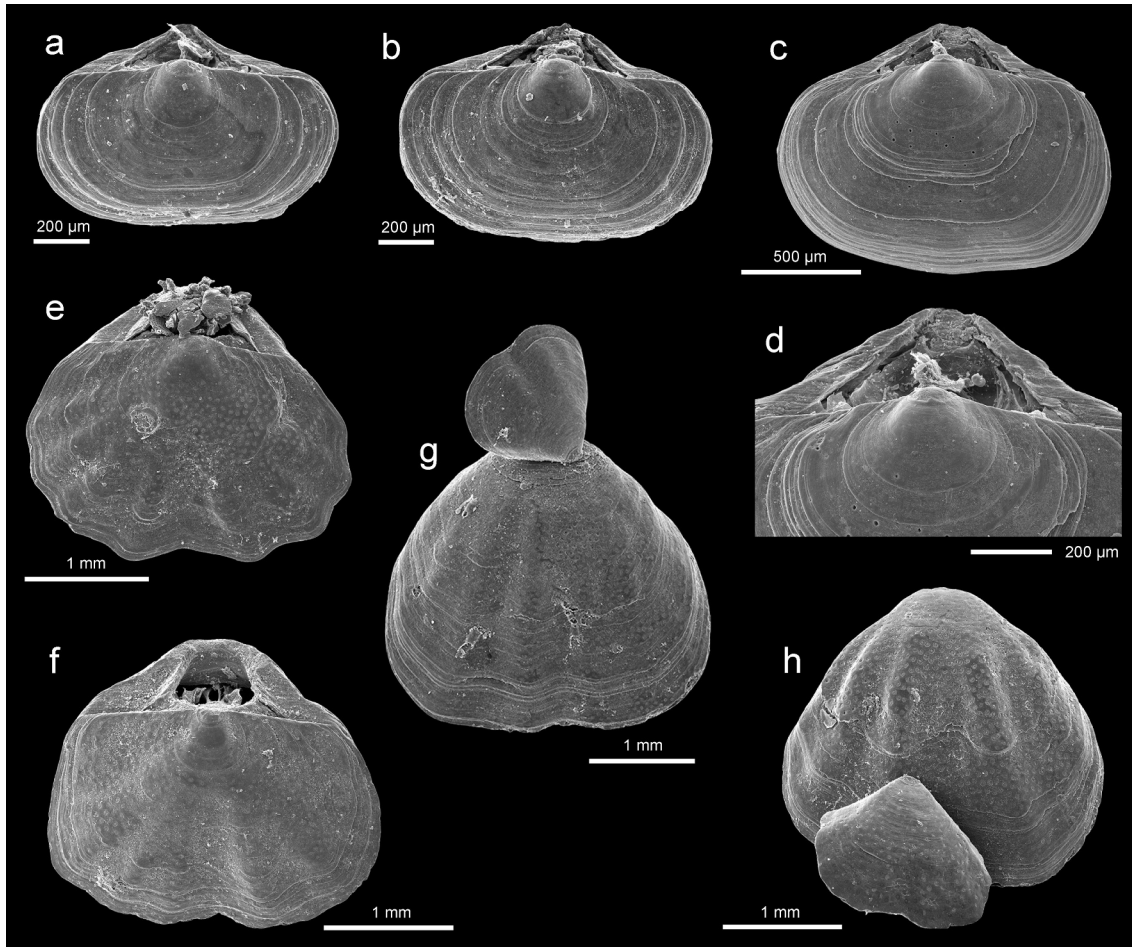


Figure 4. (a–d) *Argyrothea cistellula* (Searles–Wood, 1841): dorsal views of complete specimens and enlargement (d) of umbonal part, stations F4 (a–b) and FC2 (c–d), ZPAL Bp.85/14–16. (e–h) *Joania cordata* (Risso, 1826), station F2: (e–h) dorsal views of complete specimens, ZPAL Bp.85/16–17; (g–h) ventral views of complete specimens with attached immature individuals, ZPAL Bp.85/18–19. All SEM photos.

2020). *Joania cordata* is also common in the Northeastern Atlantic (Logan 1993).

Spatial distribution and assemblage resemblance patterns

A total of six brachiopod species were found in the two studied Aegean caves (6 in F and 5 in AV cave). Two species, *Argyrothea cuneata* and *Joania cordata* are reported from all stations while *Megathiris detruncata* was absent only from one station (F2). Only three individuals of *Tethyrhynchia mediterranea* were found on the dark wall and ceiling stations of F cave (F4 and FC2, respectively), which also exhibited the highest number of species and notably high abundance values (Tables I and II). Mean abundance differed significantly among sampling stations in both F (Pseudo- $F = 14.231$, $P < 0.01$, $df = 5$) and AV caves (Pseudo- $F = 14.995$, $P < 0.05$, $df = 3$). The highest numbers of brachiopods were recorded on the internal dark ceilings of both caves

Table II. Total species richness (S) and mean abundance (N), Shannon–Wiener diversity (H'), Simpson's diversity ($1-\lambda'$) and species evenness (J') per sampling station.

Stations	S	N	H'	J'	$1-\lambda'$
F1	3	18.3	0.202	0.184	0.114
FC1	4	7.3	0.617	0.495	0.383
F2	2	26.3	0.128	0.184	0.063
F3	3	2	0.578	0.649	0.611
F4	6	31	1.140	0.845	0.663
FC2	6	120	0.749	0.505	0.396
V1	3	27.7	0.609	0.663	0.376
VC1	4	33	0.912	0.759	0.571
V2	4	19.7	1.103	0.929	0.680
VC2	5	110	0.855	0.623	0.471

(89–144 individuals in FC2 and 85–127 individuals in VC2). On the other hand, the lowest abundance value was observed at station F3 ($N = 2$), which was characterized by high sediment cover. Variability was not

statistically significant for the two diversity indices and species evenness in the F cave. However, in the deeper AV cave, values of Shannon–Wiener (Pseudo- $F = 5.1466$, $P < 0.05$, $df = 3$) and Simpson's diversity index (Pseudo- $F = 8.2958$, $P < 0.05$, $df = 3$) differed significantly, generally being higher at the ceilings and internal wall stations (Table II).

Cluster analysis and SIMPROF test (Figure 5) showed a homogeneous composition between: (a) the outer wall stations of the two caves (Group A: F1, V1, F2; similarity 79.51%), (b) the intermediate ceiling and internal wall stations of the two caves (Group B: FC1, F4, VC1, V2; similarity 65.95%), and (c) the two internal ceiling stations (Group C: FC2, VC2; similarity 93.29%). Station F3 was differentiated from the above-mentioned groups. The species that contributed the most to the similarity of stations within the above-mentioned groups were *Joania cordata* for Group A (contrib. 74.25%) and *Argyrotheca cuneata* for Groups B (contrib. 35.1%) and C (contrib. 48.79%).

Discussion

Taxonomic composition

All six species recognized in the studied material are typical of Mediterranean marine cave environments (e.g. Rosso et al. 2013; Gerovasileiou et al. 2015;

Sanfilippo et al. 2015; Bergamin et al. 2020; Gerovasileiou & Bianchi 2021). However, in the western parts of the Mediterranean *Novocrania turbinata* is usually replaced by *N. anomala* (e.g. Taddei Ruggiero 1994, 1996, 2001; Rosso et al. 2013; Bergamin et al. 2020; Pino de la Torre et al. 2020). The latter is often present in considerable numbers, cemented on walls and ceilings of dark submarine caves where it can live in clusters (Logan et al. 2004; Radolović et al. 2015; Gerovasileiou & Bianchi 2021). A similar behaviour was also observed in the studied Aegean caves for *N. turbinata* where it contributed to the formation of nodules resulting mainly from the concretion of bryozoans and other encrusting invertebrates (Rosso et al. 2019 as *N. anomala*). The validity of the species *N. turbinata* has long been the subject of discussion (Logan 1979; Brunton 1988; Logan & Long 2001). Emig (2014) regards *N. turbinata* as a synonym of *N. anomala*. According to him the differences observed in those two species fit within the intraspecific variability. However, in his revision of the genus *Novocrania*, Robinson (2017) considers *N. turbinata* as a separate species, mostly based on a ventral valve that is strongly calcified in *N. turbinata* while in *N. anomala* the ventral valve is very thin, varying from organic to fully calcitic. The differences are also observed in the morphology of muscle scars in the interiors of dorsal valves. In *N. turbinata* anterior adductor muscle scars are elevated

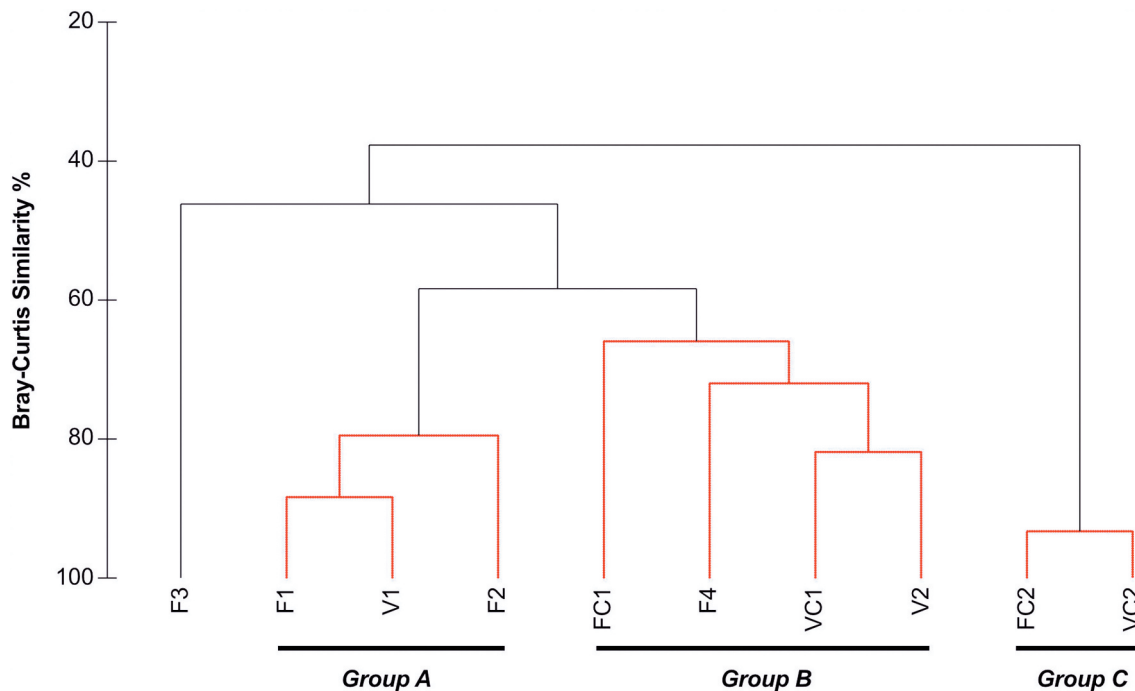


Figure 5. Resemblance of sampling stations demonstrated in Cluster Analysis dendrogram. Black lines indicate significantly different groups of samples at 5% level (SIMPROF test). Red lines indicate non-significantly different samples forming homogeneous groups. Groups A, B, and C are also indicated.

and its support structure scars (formerly brachial retractor scars; see Robinson 2014) are not separated from adductors (Logan & Long 2001; Kroh et al. 2008; Robinson 2017). Also the molecular phylogenetic analysis of craniid brachiopods seems to support the separation of those two species (Cohen et al. 2014).

The rhynchonellide *Tethyrhynchia mediterranea* is reported here for the first time from the Aegean Sea and Greek waters, increasing the regional brachiopod fauna to 13 species (Logan et al. 2002; Gerovasileiou & Bailly 2016; this study), and for the second time in the Eastern Mediterranean Sea. It was first discovered in the dark zones of submarine caves along the Mediterranean coast of France and from the Gulf of Tunis (Logan & Zibrowius 1994). Later, it was also found in caves of the Adriatic Sea, Croatia (Simon & Willems 1999; Lüter 2001; Simon et al. 2018), Sicily (Di Geronimo et al. 2001; Rosso et al. 2013; Sanfilippo et al. 2015), Cyprus (Guido et al. 2017) and southern Spain (Bergamin et al. 2020; Pino de la Torre et al. 2020). Lüter (2001) and Logan et al. (2004) suggested that *T. mediterranea* might be a relict species of the Tethyan fauna. In this study, *T. mediterranea* was found exclusively in the most confined sectors of F cave, confirming its preference for “true” cave conditions. According to the ecological groups identified by Rosso et al. (2013) for Mediterranean serpulids, bryozoans and brachiopods, *T. mediterranea* is the unique brachiopod belonging to the group of “cave species”. The remaining five species recorded in the two studied caves have been assigned to another ecological group, the “sciaphilic/coralligenous species” (Rosso et al. 2013). For instance, although *Argyrotheca cuneata* and *Joania cordata* are the most frequently reported brachiopods from Mediterranean submarine caves (Gerovasileiou & Bianchi 2021), they are also known from a wide variety of low-light habitats (Logan 1979; Gerovasileiou & Bailly 2016; Albano & Stockinger 2019).

Interestingly, the cave-dwelling brachiopods *Gwynia capsula* (Jeffreys, 1859) and *Megerlia truncata* (Linnaeus, 1767) which occur in the Greek Seas (Gerovasileiou & Bailly 2016) were not recorded in the studied caves despite the high number of samples collected.

Spatial variability and assemblage resemblance patterns

Spatial variability patterns regarding abundance and diversity were similar in both caves. Brachiopod abundance and diversity increased towards the internal confined dark zones of the studied caves, and especially on ceilings. However, the entrance zone of the deeper AV cave had higher abundance and diversity values when

compared to the equivalent zones of the shallower F cave (Tables I and II). Contrastingly, in the internal cave zones, F cave had higher abundance and diversity values than in AV cave. A similar pattern was observed for other sessile invertebrates, such as sponges (Gerovasileiou & Voultsiadou 2016), serpulid polychaetes (Sanfilippo et al. 2017) and bryozoans (Rosso et al. 2019), and was attributed to the different depth and topography of the two caves, such as entrance dimensions and internal morphology (Gerovasileiou et al. 2013).

The increase of abundance and diversity towards the internal zones of the studied caves could be possibly linked to the lower competition for space with other sedentary fauna, which is sparser in the dark cave sectors, as well as the scarcity of predators (e.g. gastropods and crabs) and absence of grazing herbivores (Taddei Ruggiero 1994, 1996). In addition, brachiopods have a very low metabolic rate compared to other marine invertebrates (Peck 2001a). The long studies carried out on the brachiopod population from Isca cave showed that in the stable cave environment *Novocrania anomala*, a species closely related to *N. turbinata*, is marked by a very slow growth, possibly reaching the age of 40 years, while the lifespan of *Argyrotheca cuneata* can be deduced to be at least 4 years (Taddei Ruggiero 1996, 2001).

Brachiopods are able to survive long periods of low food availability. Although being considered poor competitors, in cases where food supply is limited or restricted, brachiopods become very strong competitors (Peck 2001a). As shown by Bergamin et al. (2020), the abundance of brachiopods in cave sediments – where they are often found in high abundances having detached from the cave ceiling – is influenced by several factors, such as light, nutrients and water parameters. On the other hand, cave sectors with high sedimentation rates (e.g. station F3 in this study) support poorer brachiopod assemblages (Sempere-Valverde et al. 2019). This may be caused by the fact that brachiopods, as filter-feeding organisms, avoid the situation where their lophophore apparatus can be clogged by fine sediment particles.

Despite their preference for cryptic habitats, brachiopods have a minor cover in submarine caves when compared with other sessile invertebrates (Harmelin 1980; Harmelin et al. 2003; Martí et al. 2004). For instance, based on photoquadrat coverage data from a previous study in F and AV caves (Gerovasileiou et al. 2017), the mean brachiopod cover is only $0.167\% \pm 0.046$ (SE: standard error) in F cave and $0.03\% \pm 0.02$ (SE) in AV cave. In both caves the maximum brachiopod cover was observed in the internal dark ceilings and cave walls, 20–25 m away from the cave entrance

(Gerovasileiou et al. 2017). Although brachiopods were not identified at lower taxonomic ranks (except for *Novocrania* which had the highest cover among all brachiopods), due to limitations involved in the photographic identification of small-sized taxa, these findings are in agreement with the current study, where the highest abundance and diversity was recorded in the same sampling locations (Tables I and II).

Resemblance patterns for brachiopod assemblages in the two studied Aegean caves are also in agreement with those described for other sessile invertebrate taxa in the same caves, showing a clear differentiation between the outer and internal cave sectors (Gerovasileiou & Voultsiadou 2016; Sanfilippo et al. 2017; Rosso et al. 2019). Intermediate ceiling stations, characterized by a transitional assemblage between the semidark and dark cave biocoenoses (Table I, Figure 5) were grouped with the internal dark wall stations, due to the sharper decrease of light as a result of the substratum inclination (Gerovasileiou et al. 2017).

The species that contributed the most to the resemblance patterns were *Joania cordata* and *Argyrotheca cuneata*. Despite their presence in all sampling stations (Table I), *J. cordata* was more abundant in the cave entrance and semidark zones, while *A. cuneata* was very abundant in the dark parts of both caves (Table I,

Figure 6). A recent study on brachiopods from sediments in a submarine cave in southern Spain also showed that *J. cordata* was present only at the cave entrance zone (Bergamin et al. 2020). This pattern might indicate the difference in environmental preference between those two species where *J. cordata* prefers dim-light conditions, and *A. cuneata* prefers dark internal zones of caves. However, differences in breeding behaviour of *A. cuneata* and *J. cordata* may influence such differences in distribution (Grobe & Lüter 1999). Under laboratory conditions larvae in both species were observed at the same time, during October to January (Atkins 1960), however, observations by Grobe & Lüter (1999) have shown that in *J. cordata* there is no seasonality in the reproductive cycle; eggs or larvae have been observed throughout the year. On the contrary, in *A. cuneata* the larvae were found only in September and November (Grobe & Lüter 1999). As a result of endogenous development, the larvae of *A. cuneata* and *J. cordata* settle rapidly after having left the brood pouches thereby increasing the opportunities for success (Taddei Ruggiero 1994). In a fairly restricted environment like a cave, this growth pattern may not allow the larvae to travel far; this fact, coupled with a low degree of hydrodynamism, may cause gregariousness of *A. cuneata* and *J. cordata* in caves. In the examined material from the Aegean caves we have observed

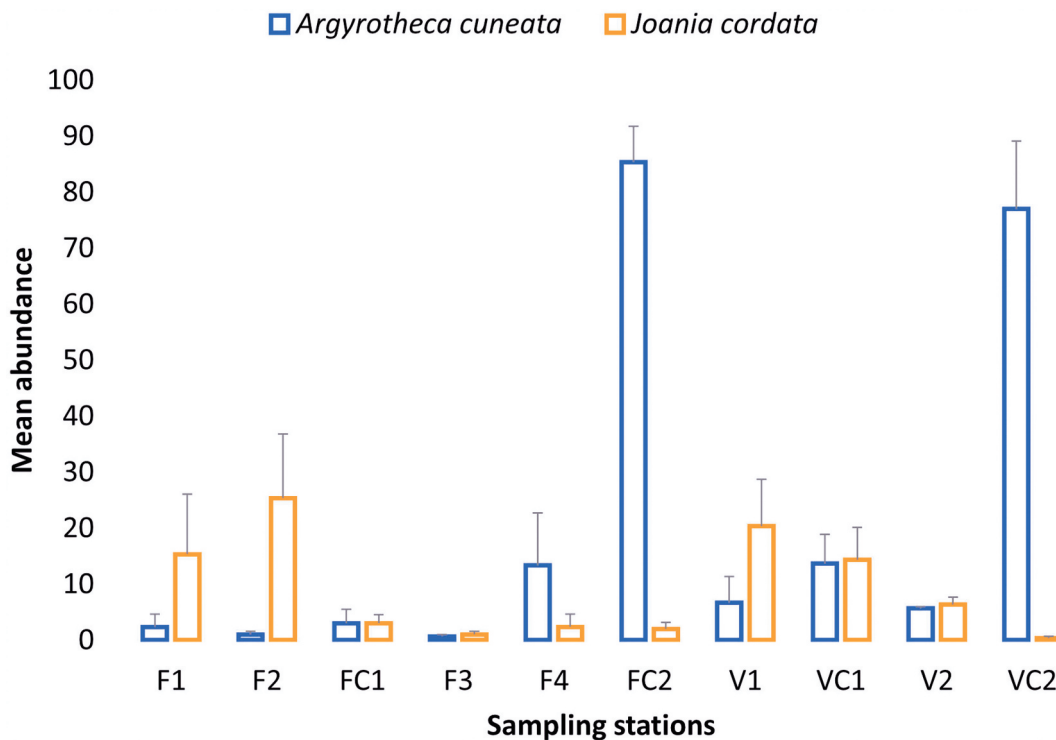


Figure 6. Mean abundance of the species *Argyrotheca cuneata* and *Joania cordata* per sampling station in the two studied caves (error bars indicate standard error).

immature individuals of *J. cordata* attached to mature specimens (Figure 4(g-h)). Preferential settlement on conspecific shells is commonly observed among articulated brachiopods (see also Figure 3(d)), especially in dense populations and when larval dispersal is limited (Peck 2001b).

Seasonal variability of sessile benthos in submarine caves has been rarely investigated (e.g. Martí et al. 2004; Bussotti et al. 2006), revealing some differences in species number and cover. The dispersal of larvae in submarine caves is determined by various factors, such as water circulation – which is generally lower in confined dark sectors (Harmelin et al. 1985; Bianchi & Morri 1994) – larval behaviour and differential post-settlement survival against environmental conditions, among others (Gerovasileiou & Bianchi 2021 and references therein). Further research is required in order to investigate the reasons behind the observed distribution patterns of these two megathyridids.

Future research in other marine caves of the Eastern Mediterranean Sea, focusing also on cave sediment thanatocoenoses, is expected to increase knowledge on the regional diversity of brachiopods and will also provide a better understanding of the spatial and temporal variability of brachiopod assemblages in the marine cave habitat.

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