Subrecent charophyte flora from Çeşmealti (Izmir Gulf, Western Turkey): Palaeoecological implications

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ABSTRACT

A charophyte assemblage from lower Holocene sediments in Çeşmealtı (Izmir Gulf, Turkey) is described and illustrated for the first time here. This assemblage is composed of well-preserved gyrogonites and oospores of *Lamprothamnium papulosum,* which occur in association with seeds of *Ruppia* cf. *maritima* and up to eight ostracod species and 22 benthic foraminiferal taxa. The fossil assemblage was extracted from five clay intervals of the SK-2 borehole. The presence of monospecific assemblages of *L. papulosum* indicates that very shallow (up to 1 m deep), brackish, alkaline, and oligotrophic waters prevailed in the gulf under strong seasonality (marked cyclical changes in humidity and/or temperature). The dominance of germinated gyrogonites suggests that the water salinity of the lagoon decreased during the humid season, reaching at least 10‰. The associated ostracod fauna supports the palaeoenvironmental conditions inferred from the flora. Despite the gulf receiving considerable freshwater input, it remained semiconnected to the sea, as indicated by the diverse foraminifera assemblage. The availability of freshwater in the Izmir Gulf during the early Holocene Climatic Optimum, between ~9000 and 5000 years BP, might have played an important role for the first human settlements in the area dating back 5500 years BP.

1. Introduction

Charophytes (Charophyta) belong to a group of aquatic plants living in shallow freshwater or brackish water environments worldwide. The fossil record of charophytes includes their calcified fructifications (gyrogonites and utricles) that have been recovered from non-marine sedimentary sequences that are as old as Silurian in age, i.e., ~420 million years (Feist et al., 2005). Their organic fructifications, i.e., oospores, can also be found in subrecent (Holocene) sediments from after 11.7 KY before present (BP) being deposited under freshwater or brackish water conditions.

Holocene gyrogonites and oospores represent a valuable tool to infer the palaeolimnological conditions of ancient waterbodies providing accurate information on palaeosalinities, water table fluctuations, and changes in the trophic status. Moreover, charophyte fructifications are biological proxies that have been employed in the reconstruction of palaeobiodiversity and the palaeoecological successions of aquatic systems. For instance, Burne et al. (1980) studied oospore banks from the sediments of recent ephemeral saline lakes in Australia to ascertain the variation in salinity over time. Soulié-Märsche (1998) and Soulié-Märsche et al. (2008) reconstructed the palaeosalinity and seasonality of several Holocene inland palaeolakes in Mauritania using gyrogonites. Moreover, García and Chivas (2004) estimated the salinity of Holocene lakes and lagoons in Western Australia using gyrogonites of *Lamprothamnium*. Soulié-Märsche (1991a) studied fossil gyrogonites from 18 Holocene localities in North Africa (Algeria, Libya, Mali, Mauritania, Niger, Senegal, and Sudan) to reconstruct the palaeolimnological conditions (water depth, temperature and salinity) of several palaeolakes. More recently, Soulié-Märsche et al. (2010) obtained significant information about the water table fluctuations of a high mountain palaeolake in Chad, relying on charophyte fructifications.

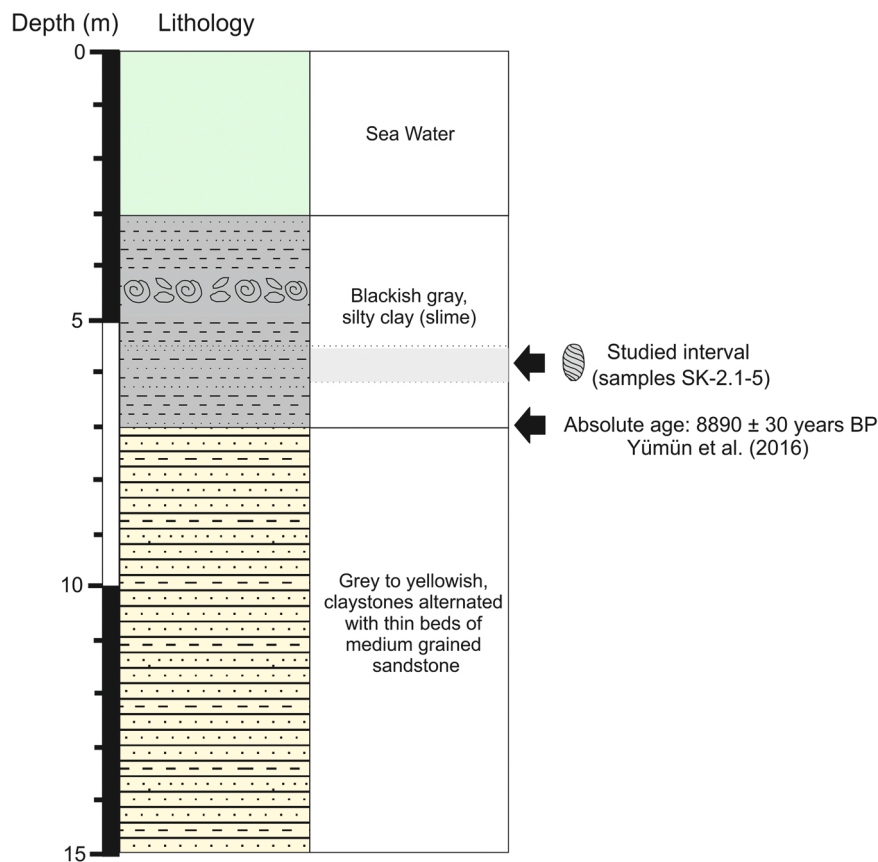This study aims to reconstruct the palaeoenvironment of the Izmir

Fig. 1. Stratigraphic log of the SK-2 borehole at Çeşmealtı (Izmir Gulf, western Turkey). Note the vertical position of the charophyte samples (between the meters 5.80 and 6.30) and the absolute dating by Yümün et al. (2016).

Gulf during the early Holocene Epoch coinciding with the Holocene Climatic Optimum (HCO), using the fossil aquatic flora. Here, we describe and illustrate the charophyte assemblage recovered from the SK-2 borehole in Çeşmealtı (Urla, Izmir Gulf, Turkey). The study of this flora helps to understand the environmental evolution of the gulf during the past millennia.

2. Materials and methods

2.1. Sample treatment and charophyte taxonomy

The studied samples were extracted from a 15-m-deep borehole (SK-2), near Çeşmealtı (Urla) in the western part of the Izmir Gulf (Turkey), UTM coordinates 4249980 N and 478300 E (Supplementary data A). The sediment core was extracted with a free-falling weighted cylindrical core barrel pesenting a diameter of 7.6 mm (Barkom brand) using a crane on a floating platform. The core was kept in specialised plastic boxes for protection and transportation. The sea water depth at the location of the SK-2 borehole was at 3 m. Forty samples, consisting of 10 g of wet sediment each, were recovered from the borehole at different depths. About 100 ml, of 10% diluted H_2O_2 were added to the samples, which were then left to stand for 24 h. The sediments were dried in an oven at 50 °C and filtered through five sieves with a mesh size of 2, 1, 0.5, 0.25, and 0.125 mm, respectively. The sieved sediments were dried and examined under a binocular microscope. The flora was extracted from five samples obtained from a narrow interval of the core, between 5.80 and 6.30 m. Yümün et al. (2016) had previously studied the other 35 samples from a micropalaeontological point of view. Several micro-fossils (charophyte remains, ostracods and foraminifera) were distinguished and sorted from the five samples. Selected gyrogonites and oospores were measured using the software Motic Images Plus 2.0 ml

software in a Motic BA310 stereomicroscope with an attached camera housed in the *Departament de Dinàmica de la Terra i de l'Oceà (Facultat de Ciències de la Terra),* University of Barcelona (Spain). The taxonomic determination of the charophyte flora was based on the biometric parameters of gyrogonites/oospores, i.e., height (μm), width (μm), number of spiral turns observed in the lateral view, and the isopolarity index (height/width × 100). For the taxonomic analysis, the systematics of Horn af Rantzien (1956) and Feist et al. (2005) were considered. These authors provided a useful set of descriptive terms based on the relationships between the gyrogonite length of the polar axis (gyrogonite height) and the equatorial diameter (gyrogonite width). Selected flora was photographed using the Quanta 200 scanning electron microscope at the *Centres Científics i Tecnològics, Universitat de Barcelona* (CCiTUB). The ostracods and foraminifers (Supplementary information B) were imaged using a Quanta 650 field emission scanning electron microscope at the Central Research Laboratory, Çukurova University (Adana, Turkey). The flora and fauna described in this study are stored at the Ege University Natural History Museum (Izmir, Turkey) and have the catalogue numbers EUNHM PV-İUC1–16 (for the flora), EUNHM PV-İUO1–16 (for the ostracods), and EUNHM PV-İUF1–5 (for the foraminifera).

2.2. Geographical and geological setting

The Gulf of İzmir is a shallow sea basin located at the north of the Karaburun Peninsula and at the south of the Aslan Cape (Western Turkey). The gulf is tectonically active and controlled by a set of faults with different trends, i.e., NE, NW, NS and EW. It geologically belongs to the Western Anatolian Extensional Province (Coşkun et al., 2017 and the reference therein). The gulf was formed during the Pleistocene and can be divided into two main parts controlled by faults: the very shallow
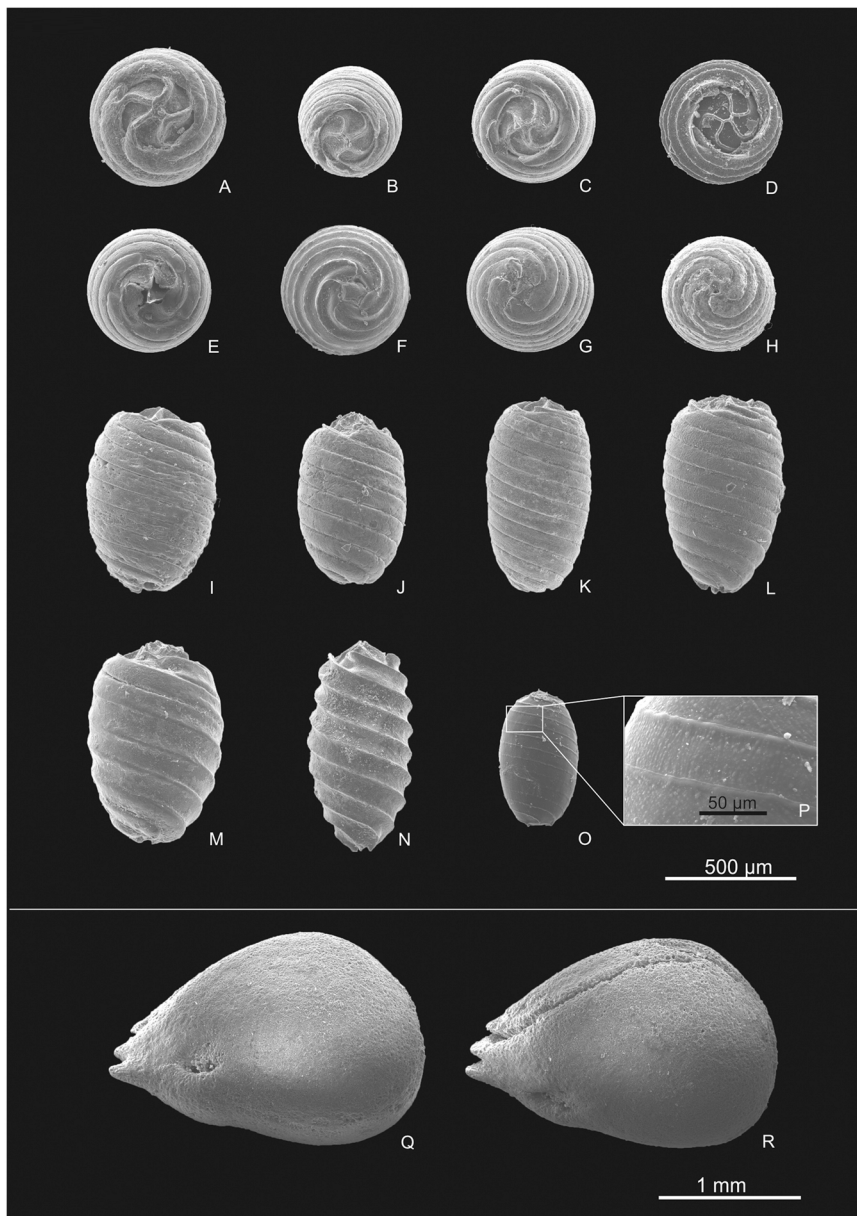
Fig. 2. Microflora assemblage from the SK-2 borehole at Çeşmealtı (İzmir Gulf, Turkey). A—N. Gyrogonites of *Lamprothamnium papulosum* from sample SK-2.3–4. A—D. apical views EUNHM PV-İUC 1–4. E—H. basal views EUNHM PV-İUC 5–8. I—N. lateral views EUNHM PV-İUC 9–14. O—P. Oospore of *Lamprothamnium papulosum* from sample SK-2.3. O. lateral view EUNHM PV-İUC 15; P. detail of the oospore's wall. Q—R. lateral views of a seed of *Ruppia* cf. *maritima* from sample SK-2.3, EUNHM PV-İUC16.

inner bay (~20 m deep), which is affected by the E-W trending faults, and the outer bay (~110 m deep) which is mainly controlled by faults with the NW trend (Aksu et al., 1990; Yılmaz et al., 2000). The inner bay forms an asymmetrical depression and the basement is composed of Upper Cretaceous-Palaeocene materials. Younger Miocene rocks (~11.6–5.3 million years old) that are covered by Pliocene-Quaternary deposits (younger than 5.3 million years old) overlie this basement. A sequence of 1500-m-thick volcano-sedimentary deposits, i.e., claystones and sandstones, represent Miocene materials. Occasionally, these rocks are folded and contain layers of coal. The younger sedimentary succession is represented by the Pliocene/Pleistocene Görece Formation (~2.58 million years old), composed of reddish sandstones and conglomerates related to an alluvial fan, as well as Holocene alluvium and shallow marine fan-delta sediments (Uzel et al., 2009). These Holocene deposits in Çeşmealtı in the area of Urla yielded the flora described in this study (Supplementary data A). According to Yümün et al. (2016), the sedimentary sequence at Çeşmealtı (SK-2 borehole) can be divided into two main intervals at different depths: (1) 3–7 m deep, shelly sandy clay that is blackish to grey in colour (Figs. 1) and (2) 7–15 m deep,

upper Miocene sandstones and claystones that are greyish/yellowish (Fig. 1). The studied flora was extracted from the 1st interval between 5.80 and 6.30 m (Fig. 1). Previous micropalaeontological studies performed in the same interval reported 22 foraminifera species and eight ostracod taxa (Yümün et al., 2016). Based on a ^{14}C radiocarbon analysis, Yümün et al. (2016) concluded that the sediments at the boundary between the two aforementioned intervals (7 m deep) date back to 8890 $\pm$ 30 years BP (Fig. 1). Since the studied interval is stratigraphically above this boundary, the age of the fossil flora described herein is younger and can be tentatively linked to the establishment of a lagoon in the gulf during the marine transgression that characterised the HCO, which ended around 6000 years BP (Goodman et al., 2009).

3. Results

Hundreds of well-preserved gyrogonites dominate the aquatic flora recovered from the SK-2 borehole in Çeşmealtı (İzmir Gulf), together with oospores of the charophyte species *Lamprothamnium papulosum* (Supplementary data C and D for systematic palaeobotany and

Table 1

Abundance of gyrogonites and oospores of *Lamprothamnium papulosum* and seeds of *Ruppia* from the SK-2 borehole at Çeşmealtı (İzmir Gulf, Turkey).

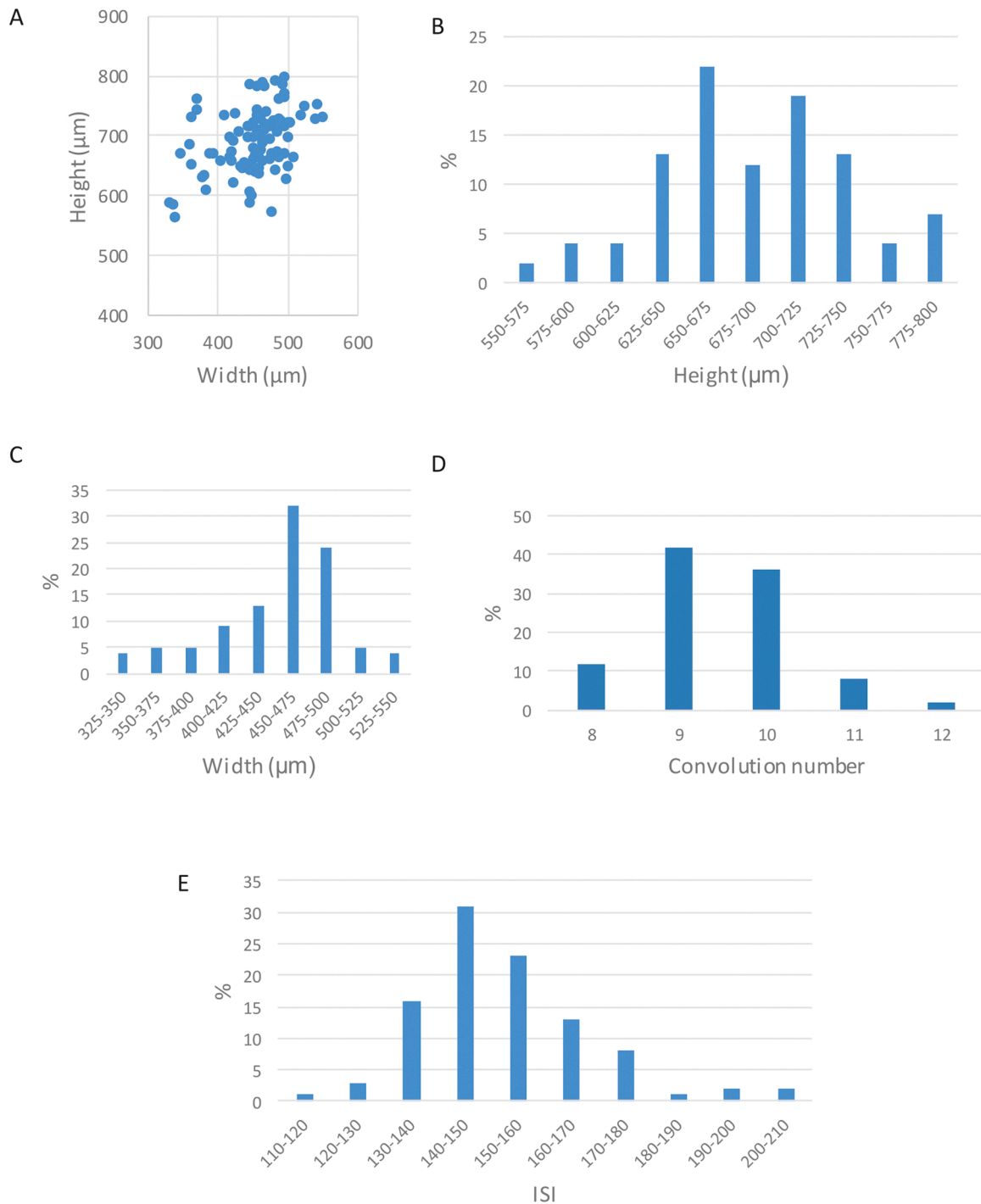| Samples, borehole SK-2	*L. papulosum* gryogonites (non-germinated)	*L. papulosum* gryogonites (germinated)	*L. papulosum* oospores	*Ruppia* Seeds
SK-2.1 (5.80–5.90 m)	34	43	7	0
SK-2.2 (5.90–6.00 m)	69	163	31	1
SK-2.3 (6.00–6.10 m)	42	146	17	4
SK-2.4 (6.10–6.20 m)	69	98	43	0
SK-2.5 (6.20–6.30 m)	1	7	1	0

Fig. 3. Biometric graphics of *Lamprothamnium papulosum* gyrogonites from samples SK-2.1 and SK-2.2 of Çeşmealtı (Izmir Gulf, Turkey). A. Dispersion graphic. B. Bar graphic showing the gyrogonite height (μm). C. Bar graphic showing the gyrogonite width (μm). D. Bar graphic showing the Isopolarity Index (ISI). E. Bar graphic showing the convolution number observed in lateral view. N = 100.

Table 2

Morphometric parameters of fossil and living gyrogonite and oospore populations of *Lamprothamnium papulosum*.

Gyrogonite Parameters	height (μm)	width (μm)	Convolution number in lateral view	Isopolarity Index (ISI)
Studied population (SK-2, İzmir Gulf)	562–797	332–550	8–12	119–204
Soulié-Märsche (1989) (Hérault, France)	525–800	350–525	*no data*	125–195
Soulié-Märsche (1989) (Bouches-du-Rhône, France)	575–775	325–525	*no data*	130–185
Oospore Parameters	**height (μm)**	**width (μm)**	**Convolution number in lateral view**	**Isopolarity Index (ISI)**
Studied population (SK-2, İzmir Gulf)	434–672	218–396	8–13	147–280
Corillon, 1972 (Charente-Maritime, France)	600–750	275–375	12–15	188–165
Krause, 1997 (Germany)	600–700	275–450	10–14	188–158

synonymy) occurring in association with the seeds of *Ruppia* cf. *maritima* (Table 1). Several gyrogonites are germinated, showing an opened apex. One hundred non-germinated specimens were measured from the samples SK-2.1 and SK-2.2 (Supplementary data E).

The gyrogonites are variable in size, ranging from 565 to 797 μm in height (mean average of 689 μm) and from 332 to 550 μm in width (mean average of 453 μm) (Fig. 3 A—C). The gyrogonites display an elliptical shape (prolate to perprolate shape following the systematics of Horn af Rantzien, 1956 and Feist et al., 2005). The isopolarity index ranges from 119 to 204, with a mean average of 153 (Fig. 3 D). Eight to 12 (frequently 9) convolutions are visible laterally (Fig. 2I—N). The spiral cells are always concave and non-ornamented, showing sharp sutures (spiral cell contact). The concavity of the spiral cells depends on the calcification degree, i.e., the spiral cells of well-calcified gyrogonites are convex, while those of low-calcified specimens are concave (Fig. 2I—N). The spiral cells range from 52 to 111 μm in height (mean average of 52 μm). The apex is flat, displaying a deep periapical furrow that forms a characteristic groove (Fig. 2A—D). The periapical region belongs to the dehiscence area during germination where the spiral cells generally become narrower or thinner (Feist et al., 2005). According to the systematics of Feist et al. (2005), this apex belongs to the lamprothamnoid-type. The base is generally rounded bearing a shallow basal pore that is pentagonal in shape and 73–104 μm in diameter (Fig. 2E—H).

The morphometrical parameters observed in the gyrogonite population (e.g., lamprothamnoid-type apex, a prolate to perprolate shape, medium size, rounded base, and shallow pentagonal basal pore) allowed them to be classified within the genus *Lamprothamnium*. The cells at the apex are markedly flattened, often depressed. At the apex periphery, they usually show very little calcification, as observed in the extant species *L. papulosum* and the fossil species *L. priscum*. Complete gyrogonites show a truncated apex with a well-marked periapical depression and a protruding centre. This apical structure usually appears opened (germinated). The populations studied in this article have similar morphometric parameters as those of previously studied gyrogonite populations of *L. papulosum* (Table 2).

Associated with these gyrogonites in the SK-2 borehole are several well-preserved oospores. Seventy-five oospores were measured from the samples SK-2.1, SK-2.2, SK-2.3, SK-2.4, and SK-2.5 (Supplementary data F).

Organic oospores are variable in size, ranging from 434 to 672 μm in height (mean average of 542 μm) and from 218 to 396 μm in width (mean average of 305 μm) (Fig. 4A—C). They are prolate in shape, with an isopolarity index ranging from 147 to 280 (mean average of 180)

(Fig. 3O—P and 5D). Eight to 13 (frequently 10) convolution marks are visible laterally (Fig. 4E), ranging in height from 36 to 70 μm (mean average of 51 μm). The oospores have a yellowish-brown glossy appearance and sometimes the starch in them can be easily observed due to their transparency. The oospore wall displays a characteristic ornamentation consisting of small granules (Fig. 2P). In other parts of the oospores, the wall is covered with pustular elevations as described by Ray et al. (2001). According to Beilby and Casanova (2014), the wall of this species displays different ornamentation types varying from grains to fibres. The morphometric parameters of the *L. papulosum* oospores studied in this work can be compared with those reported previously (Table 2).

The gyrogonite and oospore populations were found to occur in association with the endocarps (layer of the pericarp surrounding a seed in a fruit) of the aquatic plant *Ruppia* (Fig. 2Q—R), specifically the species *Ruppia maritima* Linnaeus. These endocarps are obovate to subreniform in shape (rounded kidney-shaped outline), with a smooth convex dorsal margin and a convex to sigmoidal ventral margin. An oval or round depression can be observed on each lateral side of the endocarp (Fig. 2Q—R). The dorsal germination valve is oval or narrowly triangular and slightly curved. These morphological characteristics are similar to the description provided by Zhao et al. (2004).

4. Discussion

4.1. Palaeoecology of the Izmir Gulf during the HCO

The flora and other fossil groups (benthic foraminifera and ostracods) from the SK-2 borehole in Çeşmealtı provide significant information about the palaeoecological conditions that prevailed in the İzmir Gulf during the HCO. The plant remains are composed of well-preserved gyrogonites and oospores of the charophyte species *L. papulosum* as well as the complete seeds of the macrophyte *Ruppia* cf. *maritima*. The preservation status of these remains indicates autochthony.

The euryhaline species *L. papulosum* thrives in brackish waters with varying salinities, from seawater to freshwater (Daniel, 1975; Moore, 1986). This species can tolerate a wide range of salinities from very diluted brackish waters with a salinity of 1‰ to hypersaline waters with salinities of up to 95‰ (Bisson and Kirst, 1983 and references therein). It normally thrives in saline conditions, where salinity gradually increases due to evaporation during the season. Laboratory experiments indicate that *L. papulosum* grows best at salinities between 8‰ and 28‰ (Daniel, 1975). The plant is fertile and produces viable oospores at salinities ranging from 20‰ to 40‰ (Soulié-Märsche, 1998, 2008). For gyrogonites/oospores to germinate, at least three months of this salinity range is required (Soulié-Märsche, 1998). However, they preferably germinate at salinities of about 10‰ (Dubois, 1968). According to Soulié-Märsche (1998), *L. papulosum* requires changes in salinity to grow and reproduce (seasonality) and cannot tolerate permanently fresh nor permanently highly saline waters. In Europe, mature oospores can be found as early as April (Mouronval et al., 2015). It is considered an annual species and survives as oospores and bulbils during the drying-out summer season. It sprouts a few weeks after the autumn or winter rains. However, the plant can overwinter in a vegetative way in permanent waterbodies, even in hypersaline environments (Burne et al., 1980) and inhabits warm, alkaline, oligo-mesotrophic, and shallow waters at depths of between 5 and 100 cm. According to Blindow and Langangen (1995), the plant prefers fine-grained sediments, mainly a mixture of sand and silt. This taxon thrives in a wide array of habitats from temporary ponds to permanent lagoons surrounded by halophilic vegetation such as *Salicornia* (Mouronval et al., 2015). Moreover, *L. papulosum* is sensitive to eutrophication and the increase in nutrients in several habitats due to human activities which makes its occurrence scarce. A few seeds of *Ruppia* cf. *maritima* Linnaeus (Ruppiaceae) were found in two samples from the borehole (Table 1). *Ruppia* is a cosmopolitan genus of aquatic plants living in estuaries and brackish water environments. *Ruppia* can live in
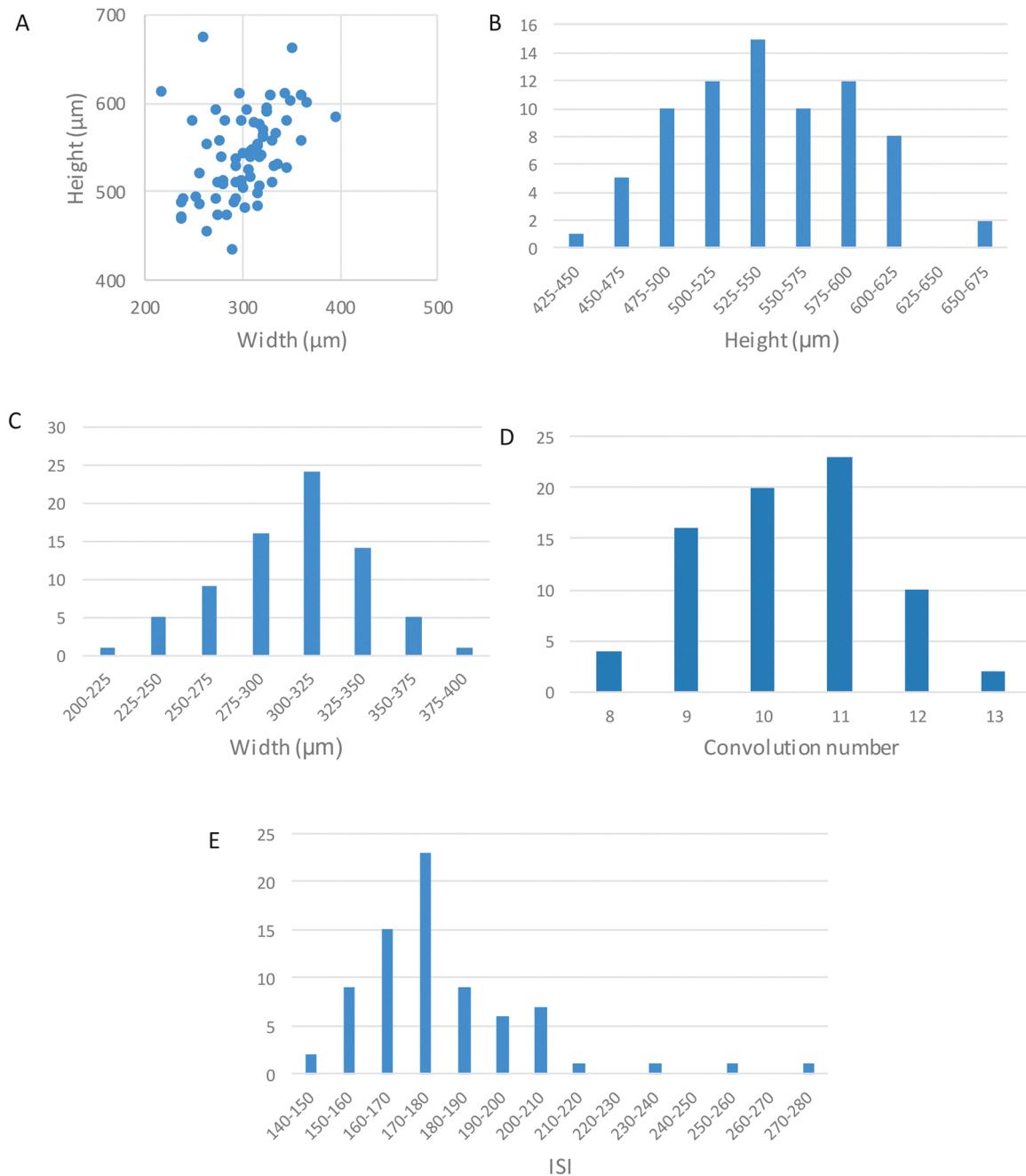
Fig. 4. Biometric graphics of oospores of *Lamprothamnium papulosum* from samples SK-2.1, SK-2.2, SK-2.3, SK-2.4 and SK-2.5 of Çeşmealtı (Izmir Gulf, Turkey). A. Dispersion graphic. B. Bar graphic showing the oospore height (μm). C. Bar graphic showing the oospore width (μm). D. Bar graphic showing the Isopolarity Index (ISI). E. Bar graphic showing the convolution number observed in lateral view. N = 75.

coastal water bodies, including lagoons, estuaries, abandoned salt flats, and aquaculture ponds. Species of *Ruppia* can live at depths of between 30 and 200 cm (Yu and den Hartog, 2014). Endemic to the Mediterranean, species of this genus have also been reported in South Africa, Finland, Anatom Island (Vanuatu), Yu-Hong, (China), Maharashtra (India), Cape Breton Island (Nova Scotia, Canada), the Strzelecki Track (South Australia), and the Indian River Lagoon (USA) (Peek and Clementz, 2012; Ito et al., 2013).

The dominance of *L. papulosum* in the studied interval indicates that very shallow (up to 1 m deep) brackish water as well as alkaline and oligotrophic conditions prevailed in the gulf during the HCO. Moreover, the absence of other charophyte species in the microfossil assemblage suggests that strong salinity fluctuations (from 10‰ to 40‰ to hypersaline) and seasonality occurred in the area. The high occurrence of

germinated gyrogonites indicates that the water salinity decreased during the humid seasons, reaching at least 10‰. The ecological requirements of *Ruppia maritima* are consistent with those of *L. papulosum*.

Up to 54 foraminifera species and 32 ostracod taxa were extracted from the SK-2 borehole by Nazik et al. (2014) and Yümün et al. (2016). However, only 22 foraminifera and 8 ostracod species were observed to be associated with *L. papulosum* at the depth between 5.80 and 6.30 m (Supplementary data G). The foraminifera assemblage at this depth is dominated by 8 species: *Spiroloculina ornata* (d'Orbigny), *Peneroplis pertusus* (Forsskål in Niebuhr), *P. planatus* (Fichtel and Moll), *Pseudotriloculina oblonga* (Montagu), *Ammonia parkinsoniana* (d'Orbigny), *A. compacta* (Hofker), *A. tepida* (Cushman), and *Elphidium crispum* (Linnaeus). The four most abundant species of foraminifera are illustrated in supplementary data B. Four freshwater and brackish water

ostracods are also common in this charophyte-rich interval (Supplementary data G): *Cyprideis torosa* (Jones), *Loxoconcha elliptica* (Brady), *Heterocypris salina* (Brady), and *Ilyocypris bradyi* (Sars). Other marine and lagoonal taxa such as *Loxoconcha bairdi* (Müller), *L. stellifera* (Müller), *Xestoleberis communis* (Müller), and *Callistocythere* sp. have also been recovered (Supplementary data B).

Together, these findings indicate that the Izmir Gulf at Urla during the HCO formed a brackish water lagoon with maximum depth of 1 m and salinities ranging from 20‰ to 40‰, being occasionally 10‰ for at least 3 months. These conditions allowed the development of dense *L. papulosum* stands. The associated fauna (foraminifera and marine ostracods) suggests that the lagoon displayed intermittent connections to the sea. The inferred palaeoenvironmental conditions of the Izmir Gulf during the HCO are in contrast to the current ones, i.e., 3 m deep and a permanently saline marine bay.

4.2. Fossil record and palaeobiogeography of L. papulosum

The genus *Lamprothamnium* originated during the Early Cretaceous (Feist and Grambast-Fessard, 1991). However, the oldest population attributed to *L. papulosum* (originally named *L. priscum*) was found in Lower Eocene rocks (~48 million years old) in the Corbières area, south of France (Castel and Grambast, 1969). Fossil populations of *L. papulosum* have been recovered from Pliocene to upper Holocene deposits in France (Soulié-Märsche, 1989), North Africa (Soulié-Märsche, 1982, 1991a; b, 1993), and Australia (García and Chivas, 2004). *L. papulosum* is now a cosmopolitan species thriving in brackish water habitats in Europe, Africa, Asia, and Oceania. In Europe it has been found in Italy, Greece, Spain, France, England, Germany (Baltic coast), Denmark, Norway, and Sweden (Olsen, 1944; Moore, 1986). In Sweden, *L. papulosum* has only been observed at the west coast. Its absence from the east coast is probably due to the low salinity of the Baltic Sea (Blindow and Langangen, 1995). Despite this species not being recurrent in Asia, it has been reported to occur in a few disjunctive localities in China, India, Pakistan, and Bangladesh (Naz et al., 2010 and the references therein). Meadows of this charophyte have also been observed in North Africa (Morocco, Tunisia, and Algeria) (Guerlesquin, 1992 and the references therein). This species has also been detected in South Africa (Port Elizabeth) as well as in Australia and New Zealand (Casanova, 2013 and the references therein). Although living meadows of this taxon have not been reported yet in western Anatolia, subrecent gyrogonite populations of *L.* cf. *papulosum* have been found by Bassler-Veit et al. (2013) in three localities: the Gökçeada Island Salt Lake, the Enez Salt Lake, and the Kavak (Uzungöl) Lagoon. This study confirms the occurrence of *L. papulosum* in the Holocene Izmir Gulf.

4.3. Implications for human settlements and regional climate during the HCO

Although the Holocene sedimentary sequence extracted from the SK-2 borehole is dominated by marine deposits, the fossils extracted from the studied interval (between 5.80 and 6.30 m) reveal the existence of a lagoon with significant freshwater input. This freshwater input might have played an important role in the human settlements in the gulf during the past millennia (e.g., food production, fishing, irrigation). The oldest archaeological site (human settlement) near the studied SK-2 borehole in Çeşmealtı is the Liman Tepe (Iskele, Izmir), which is Late Chalcolithic in age (5500 years BP). The Liman Tepe was an important point for trading, connecting both the Mediterranean and Aegean seas to the Asian continent during the Chalcolithic and early Bronze Age (Erkanal, 2008; Erkanal and Şahoğlu, 2016). Since then, humans have continuously occupied the gulf (Erkanal, 1995 and the references therein). The date of these first human settlements and the establishment of a lagoon in the region seem to overlap. According to Goodman et al. (2009), the marine transgression that took place after the Last Glacial Maximum ended around 6000 years BP, when the sea level reached its modern status, promoting the development of sandbanks, coastal barriers and eventually the near-shore lagoons in the gulf.

The development of a brackish water lagoon in Çeşmealtı indicates that the gulf received considerable freshwater input, which is essential for human communities to develop. This event can be tentatively correlated with a Holocene humid climatic phase or the HCO. Palynological studies suggest that a humid and warm climate phase took place in the eastern Mediterranean between 9000 and 6000 years BP, after the Younger Dryas Glaciation (Rossignol-Strick, 1995 and the references therein).

In conclusion, we describe and illustrate for the first time here a subrecent charophyte assemblage composed of well-preserved gyrogonites and oospores of the cosmopolitan brackish water species *Lamprothamnium papulosum* from the Gulf of Izmir (Turkey). These gyrogonites and oospores were found to occur in association with the seeds of *Ruppia* cf. *maritima*, as well as brackish-water and marine ostracods and benthic foraminifera. The microfossil assemblage was extracted from a clay interval of the SK-2 borehole (Çeşmealtı), which can be tentatively linked to the marine transgression that characterised the Holocene Climatic Optimum that ended around 6000 years BP. The occurrence of *L. papulosum* indicates that a brackish water environment (estuary or lagoon) had developed in the gulf then. It was very shallow (up to 1 m deep), alkaline, and oligotrophic, and subjected to seasonality. The high percentage of germinated gyrogonites within the studied assemblage suggests that the palaeosalinity reached a minimum of 10‰. In summary, this study proves that a very shallow brackish water lagoon stood in the western part of the Izmir Gulf during the HCO, coinciding with the establishment of the first human settlements in the area.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

I've shared the data in the attached files.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2022.103613.

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