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SHORT COMMUNICATION

An Unusual Protuberant *Lithophyllum* sp. From Southern Spain Increases Structural Complexity in Urchin Barrens

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ABSTRACT

Urchin barrens ('blanquizales') are habitats dominated by encrusting non-geniculate coralline algae and maintained by urchin grazing. Taxonomic information of coralline communities in Mediterranean blanquizales is limited. Lumpy to fruticose coralline algal specimens, unusual in blanquizales, were found along the southern Spanish coast. Sequences from these specimens resolved with foliose samples morpho-anatomically identified as *Lithophyllum dentatum*. Initial observations suggested that this protuberant *Lithophyllum* species increases diversity in the otherwise species-poor exposed blanquizales. When present, higher macroalgal cover was observed with algae and microfauna frequently observed as epibiotic among the coralline's protuberances.

1 | Introduction

Non-geniculate coralline algae are prominent components of Mediterranean marine habitats, including coralline rims or trottoirs, vermetid reefs and coralligenous, rhodolith or maerl beds (Templado et al. 2012). They have high conservation value because of the diversity they support through the provisioning of complex three-dimensional structures (Amado-Filho et al. 2010; Ingrosso et al. 2018). In contrast, urchin barrens, or 'blanquizales', are subtidal habitats also dominated by non-geniculate coralline algae, but with encrusting growth forms and therefore considered flat, featureless (i.e., low complexity) environments, consequently supporting less diversity that other coralline algal bioconstructions (Pinna et al. 2020).

Mediterranean blanquizales develop from the overgrazing of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, which severely limits the growth of fleshy macroalgae, resulting in bare substrates totally or partially covered by mostly encrusting non-geniculate coralline algae (Templado et al. 2012; Bulleri 2013). Blanquizales research was most active in the northern Mediterranean (Northern Spain, France, Italy, Croatia) where the focus was on distribution mapping, sea urchin dynamics and associated faunal diversity (Maggiore et al. 1987; Palacín et al. 1998; Bulleri 2013; Pinna et al. 2020; Cvitković et al. 2024). An underlying concern of these studies was the prevention or management of the phase shift from complex vegetated habitats into species-poor blanquizales.

Non-geniculate coralline algae, despite being the dominant benthic organism, have not been the focus of any taxonomic or ecological research in the Mediterranean blanquizales. Detailed information on coralline algal diversity in these habitats is, however, available from the Canary Islands (Afonso-Carrillo 1983, 2021) just outside the Mediterranean, but these studies are based solely on morpho-anatomical identifications. Sequence data have become an important component of coralline algal taxonomy, as cryptic species are abundant

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in this group (Hind et al. 2016; Gabrielson, Hughey, and Diaz-Pulido 2018; Caragnano et al. 2020; Puckree-Padua, Gabrielson, and Maneveldt 2021). Without DNA sequences, especially from decades-old type specimens, crypticity in corallines is an obstacle to accurate identifications and representation of species distributions, which are essential in conservation planning.

Examining blanquizales in southern Spain revealed several unusual, attached, protuberant non-geniculate coralline algal specimens. Initial investigations suggested they belonged to the same species, and more importantly, that they were a unique morphotype in a clade of coralline algae containing foliose thalli. This study provides a preliminary characterization of the environments where these protuberant thalli were observed and a detailed description of this morphotype in Mediterranean blanquizales using both DNA sequence and morpho-anatomical data.

2 | Methods

2.1 | Study Sites

Blanquizales with attached, lumpy to fruticose non-geniculate coralline algal thalli were observed from several locations along the southern coast of Spain (Figure 1A–D), including: Caleta de Vélez (36.7474339 N, 4.073061911 W), Peñón de San Cristobal, Almuñecar (36.72850914 N, 3.693611799 W), Caleta de Salobreña (36.74431754 N, 3.602396841 W) and Azucenas Beach, Motril (36.71594766 N, 3.508232876 W). The study sites are classified under codes 03010309, MB1511 and MB1.518a describing blanquizales environments in the Spanish inventory of marine habitats (Templado et al. 2012), the European Nature Information System (EUNIS) database and the Barcelona Convention, respectively.

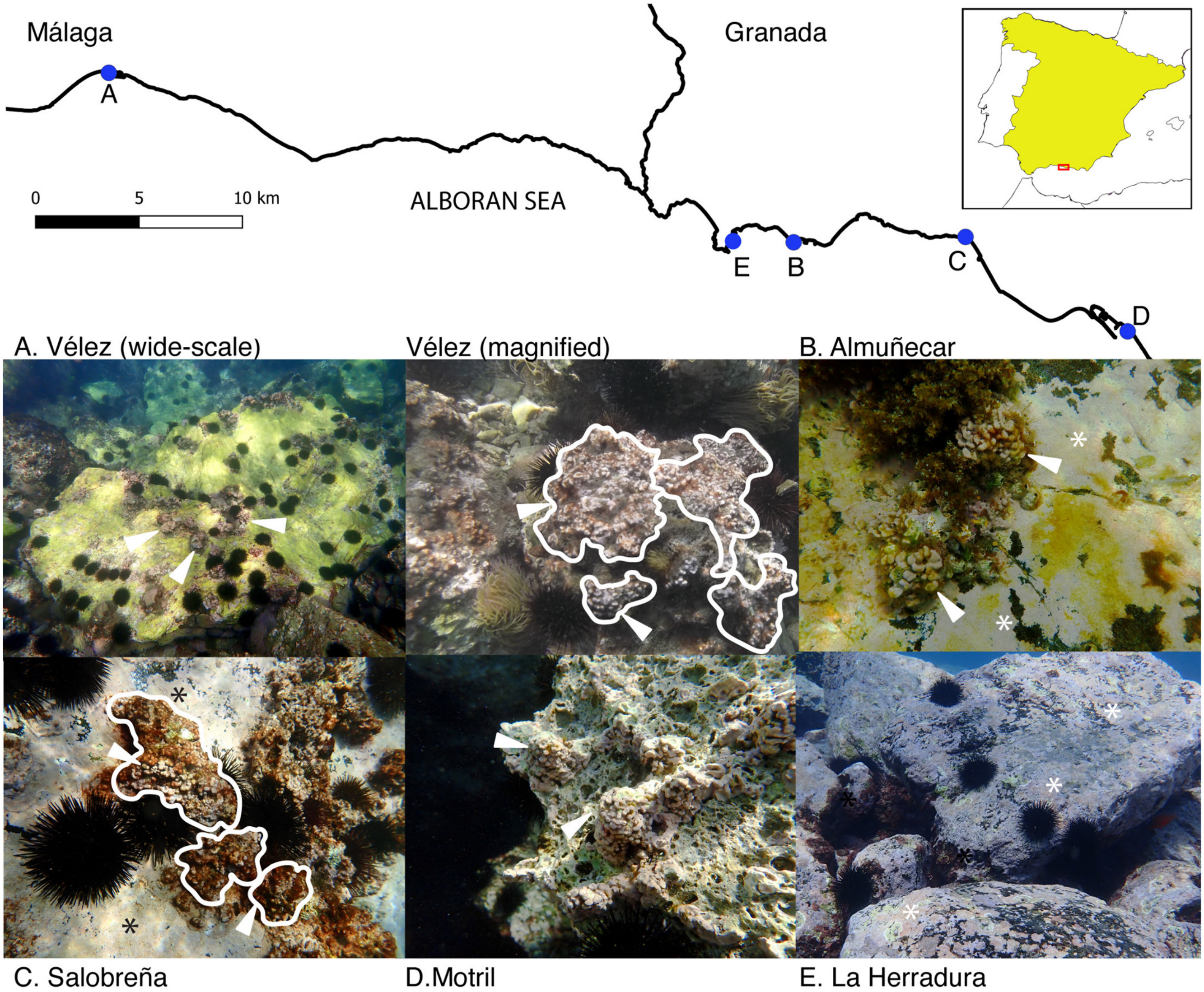

FIGURE 1 | Localities of blanquizales environments along the southern Spanish coast (A–E). La Herradura (E) lacks the protuberant thalli. Inset shows the location of the sites (red box) in Spain (yellow). In situ photographs of the protuberant thalli (arrowheads and outlines). Encrusting coralline algae (asterisks) are usually dominant in blanquizales.

2.2 | Data Collection

Samples of protuberant specimens were collected using a dive knife. The environments around the samples were photographed with an Olympus TG-5 (Tokyo, Japan) digital camera. Five images per site were used to quantify the relative benthic cover. Component proportions were estimated by counting 180 points over a 30 cm × 30 cm quadrat with the random point-counting tool of JMicroVision 1.3.1 software (Roduit 2007). The following components were distinguished: (1) protuberant corallines, (2) encrusting corallines, (3) fleshy and geniculate algae, (4) turf algae and microbial mats, (5) sea urchins, (6) other invertebrates and (7) unknown for points that could not be identified from photos. These components were compared with images of blanquizales from Punta del Vapor, La Herradura where only encrusting non-geniculate corallines were present (Figure 1E and Table S1).

2.3 | Coralline Identification

Samples were air dried in a dark environment after collection. Part of the surface was scraped with a surgical blade to remove epiphytes, then pulverized for DNA extraction with a Dremel 4250 rotary tool (Illinois, USA) with a diamond wheel point. The Macherey-Nagel NucleoSpin 96 Tissue Core Kit was used for DNA extraction following the manufacturer's instructions. The *psb*A and COI-5P barcodes were amplified and sequenced with the psbA-F1/psbA600R primers (Yoon, Hackett, and Bhattacharya 2002) and the GazF1/GazR1 primers (Saunders 2005), respectively. Marker amplification followed Ramos et al. (2024). PCR products were sent to Eurofins Scientific (Nantes, France) for purification and sequencing.

Sequences were assembled and aligned using CodonCode Aligner 10.0.3. Sequences were successfully obtained from two of four samples. A basic local alignment search tool (BLAST) query identified the new sequences as belonging to a species of *Lithophyllum*. Type-linked and non-type *Lithophyllum* sequences (*psb*A and COI-5P) from GenBank were aligned with the new sequences. *Porolithon*, *Harveylithon*, *Chamberlainium* (*psb*A) and *Parvicellularium* (COI-5P) sequences were selected as outgroups. Percent sequence divergence (p-distance) was calculated using MEGA 11 (Tamura, Stecher, and Kumar 2021). Maximum likelihood (ML) trees were generated in iqtree 2.2.2.7 (Minh et al. 2020) using the best model (*psb*A: GTR + F + I + G4; COI-5P: TIM + F + I + G4) selected by ModelFinder (Kalyaanamoorthy et al. 2017) and ran for 1000 bootstrap replications (Figures S1 and S2). A Bayesian inference (BI) tree was produced with MrBayes 3.2.7 (Ronquist et al. 2012) running the GTR + I + G model (MCMC: 2,000,000 generations, sampling every 1000 generations, burn in: 25%). Figure 2 presents extracts of the ML trees including the node support values of the equivalent clades from the BI tree. Two species delimitation algorithms were used for both marker datasets: (1) assemble species by automatic partitioning or ASAP (Puillandre, Brouillet, and Achaz 2021) and (2) Bayesian implementation of the Poisson tree process or bPTP (Zhang et al. 2013). The two highest ranked delimitations from ASAP and the Bayesian delimitation from bPTP are presented.

Anatomical images of thallus fragments were produced with an FEI Field Emission Gun Scanning Electron Microscope QemScan650F (Hillsborough, USA) following Ramos et al. (2024). Anatomical features were measured using ImageJ (Schneider, Rasband, and Eliceiri 2012) according to the conventions of Irvine and Chamberlain (1994). Growth form descriptions followed Woelkerling, Irvine, and Harvey (1993). Samples were deposited at the University of Granada Herbarium (GDA). Herbarium acronyms followed Thiers (2024).

2.4 | Statistical Analysis

RStudio 2024.09.0 with the vegan and pairwiseAdonis packages was used for all analyses. A Bray-Curtis distance matrix was generated from percent cover data (presented in the results as mean ± SD) of benthic components for each photoquadrat. PERMANOVA was used to check for significant differences ($p < 0.05$) in benthic composition across sites using this matrix and pairwise PERMANOVA as the post hoc test. An NMDS plot visualized the benthic components responsible for the differences observed (Figure S3).

3 | Results

3.1 | Site Descriptions

All sites were partially protected from wave exposure by natural or artificial barriers (i.e., port structures, cliffs and crags). Encrusting non-geniculate coralline algae were dominant on the available substrate, except for Vélez where protuberant non-geniculate coralline algae were more abundant. The protuberant thalli were photophilous, growing on subtidal rocky substrates between 0.5 and 2.5 m.

3.2 | Cover Abundance

Benthic composition differed significantly across all sites (pairwise *p*-values: 0.004–0.032). Encrusting corallines were dominant in the study sites apart from Vélez (4.2 ± 3.0%), reaching 62.8 ± 17.7% in typical blanquizales. The relative cover of protuberant thalli in sites A–D was highest in Salobreña (27.6 ± 9.6%) and lowest in Almuñecar (9.8 ± 5.7%). Urchins, fleshy and geniculate algal abundance generally increased in sites with protuberant thalli (Table S1 and Figure S3). Turf algae was the most variable component, ranging from 2.4 ± 1.5% to 42.8 ± 17.7%. Other invertebrates such as barnacles (e.g., *Perforatus perforatus* and *Balanus trigonus*) and anemones (e.g., *Anemonia viridis* and *Aiptasia mutabilis*) comprised a minor proportion of the benthic cover (0.2 ± 0.4%–3.8 ± 6.9%).

3.3 | Protuberant *Lithophyllum* Thalli

A *psbA* (GDA 73872: PQ593847) and COI-5P (GDA 73873: PQ593846) sequence was obtained from protuberant thalli. Our sequences resolved with those from samples that were

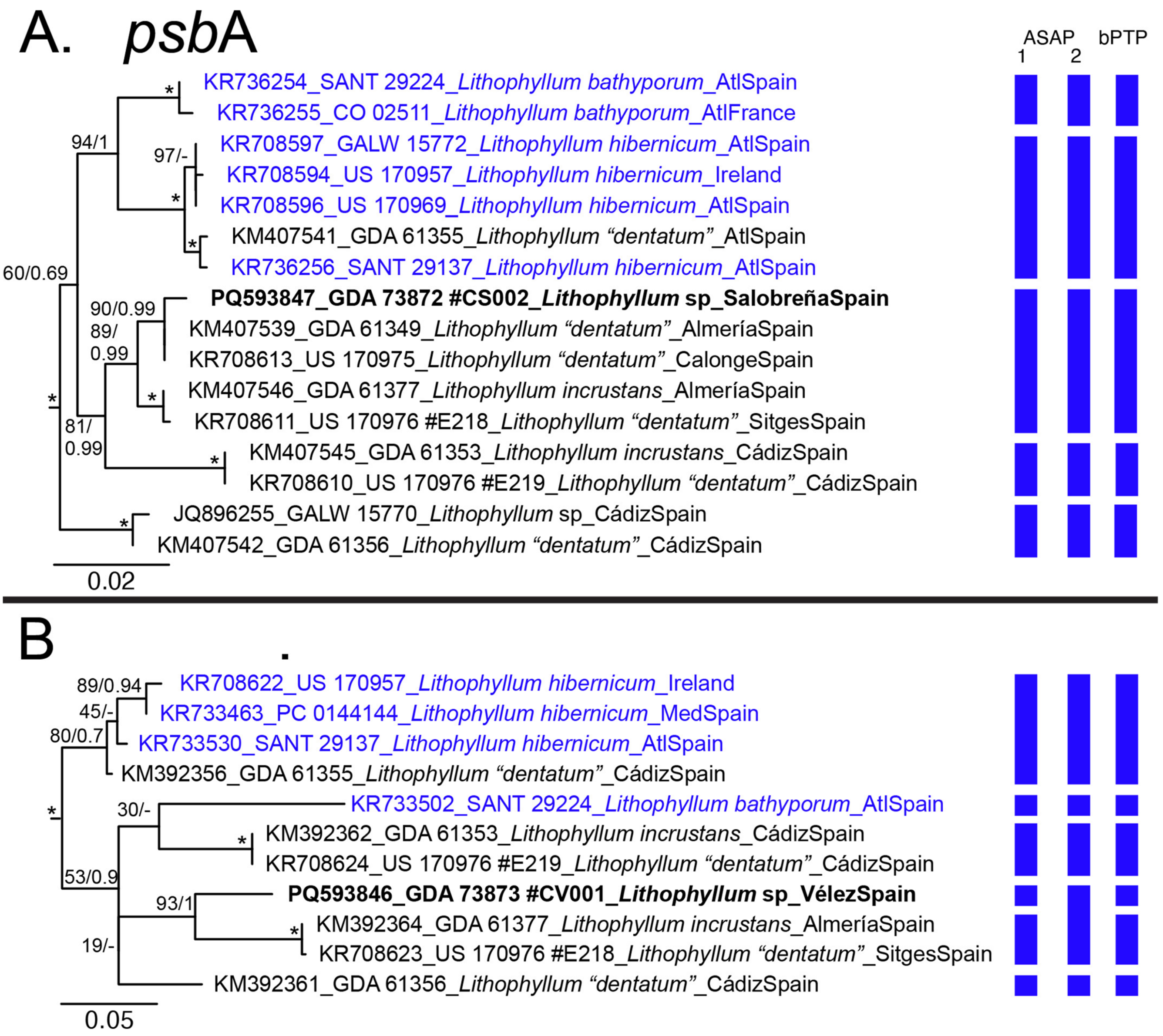

FIGURE 2 | Extracted clades from *Lithophyllum* trees containing the protuberant thalli sequences. Sequences are labelled by GenBankAccession_HerbariumAccession_Identification_Locality. Collection codes (#) specify the sequenced sample for herbarium accessions with multiple specimens. The *psb*A (A) and COI-5P (B) sequences from this study are in bold. Sequences in blue were previously linked to types; all other sequences were from specimens morpho-anatomically identified as such. Asterisks denote node support values ≥ 95/0.95 (bootstrap/posterior probability); dashes (–) are clades absent from the Bayesian tree. Vertical blue bars illustrate species delimitations.

morpho-anatomically identified as *Lithophyllum dentatum* (Kützing) Foslie and *Lithophyllum incrustans* Philippi (Figure 2). Species delimitations proposed two to three other species with *L*. '*dentatum*' sequences—in quotations since there are no confirmed type sequences for the species. The more conservative ASAP 2 delimitation that considered all Mediterranean sequences the same species resulted in intraspecific sequence divergences of up to 1.08% for *psb*A and 6.47% for COI-5*P*. Interspecific sequence divergence ranged from 2.15% to 4.29% for *psb*A and 6.54% to 10.39% for COI-5P.

The studied coralline specimens range from isolated (Figure 1D) to densely grouped pink to purple thalli (Figure 1A,C, white outlines) that develop thick protuberances (Figure 1C), which tended to fuse laterally. Protuberances typically reached 3–5 cm in height (Figure 3A) but often extended to 10–12 cm. Mytiloids, *Leiosolenus aristatus*, bored into the thallus while chitons, *Rhyssoplax olivacea*, were found in between branches.

Cells of adjacent filaments were well-aligned and connected by secondary pit connections (Figure 3B). Tetra/bisporangial conceptacles were slightly raised above (Figure 3C), flush with or sunken below the thallus surface (Figure 3D). Buried conceptacles with a prominent central columella and a cylindrical pore canal were present (Figure 3D,E). Tetra/bisporangial chambers were 161–304 μm in diameter and 60–146 μm in height (Table S2).

4 | Discussion

This study reports on a protuberant species of *Lithophyllum* previously undocumented from blanquizales in the

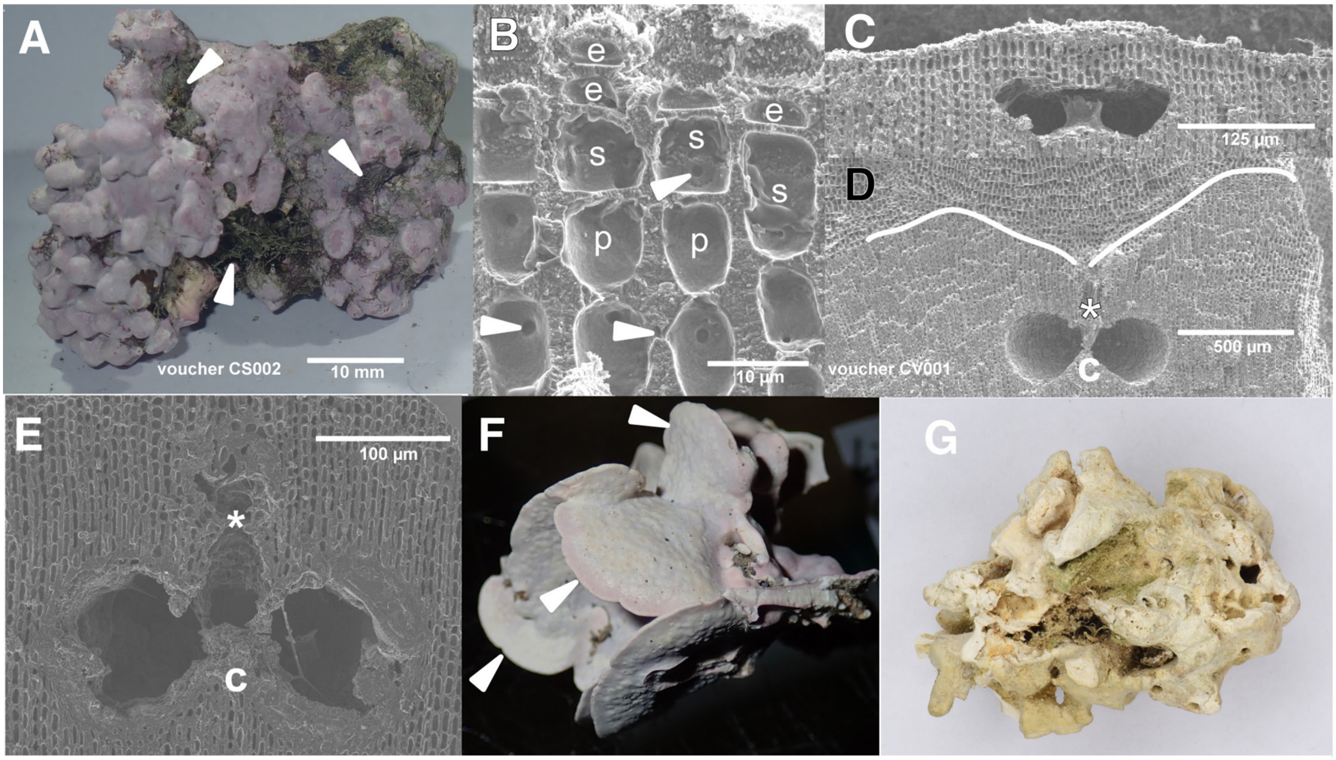

FIGURE 3 | Images of the sequenced protuberant *Lithophyllum* sp., GDA 73872 (A–C) and GDA 73873 (D–E); a foliose *L.* '*dentatum*', GDA 61349 (F); and the *L. dentatum* lectotype, L0063104, formerly designated L943.7.69 (G). (A) *Lithophyllum* sp. showing the thick, protuberant thallus. Filamentous algae can be seen growing in the crevices between branches (arrowheads); (B) section of the thallus surface showing the secondary pit connections (arrowheads), epithallial (e), subepithallial (s) and cortical (p) cells; (C) conceptacle slightly protruding from the surface; (D) older thallus surface outlined in white to show the sunken conceptacle with a columella (c) and columnar pore canal (*); (E) buried conceptacle with bean-shaped chambers, columella (c) and columnar pore canal (*); (F) *Lithophyllum* '*dentatum*' thallus consisting of thin lamellae (arrowheads); (G) irregular branches of the *L. dentatum* lectotype (photo: Roxali Bijmoer).

Mediterranean and part of a *L.* '*dentatum*' species complex. We cannot determine if the true *L. dentatum* is represented in the species complex without confirmed type sequences. In her PhD studies, Hernández-Kantún (2013, chapter 3) reported an *rbc*L sequence from the type of *L. dentatum* (locality: Naples, Italy) but it was not made not publicly available in repositories like GenBank. Samples from Spain matching that *rbc*L sequence had corresponding *psb*A and COI-5P sequences (KR708613, KR708611 and KR708623), which resolved with other Mediterranean sequences, including the protuberant *Lithophyllum* sp. However, the reported *rbc*L type sequence was later omitted by Hernández-Kantún et al. (2015) while advocating for the need to resolve the identity of *L. dentatum*. This suggests that there may have been problems with the sequence reported in the thesis and so we did not consider it a valid type sequence.

The *psb*A delimitations grouped all Mediterranean sequences of the *L.* '*dentatum*' complex together, but COI-5P data suggest that our specimens are likely a different species. Two of the COI-5P delimitations separated PQ593846 from other Mediterranean sequences with a divergence of (6.47%), higher than the intraspecies divergence (3.8%) reported for *Lithophyllum kuroshioense* A. Kato & M. Baba (2019). After the reassignment of *L.* '*dentatum*' from Ireland to *L. incrustans* (Hernández-Kantún et al. 2015), all remaining sequences attributed to this species are from Spain. Further sampling is needed across its reported range in the Mediterranean, especially in its type locality, and North Atlantic to understand its genetic, morphological and ecological variability.

Morphological identification of *L. dentatum* using the foliose morphology (Figure 3F) has probably resulted in misidentifications and the polyphyletic distributions of sequences identified as such. The foliose growth form has not been associated with the *L. dentatum* type but has been linked with confirmed sequences of *L. incrustans* (KP030737—Figure S1; Hernández-Kantún et al. 2015) and *L. hibernicum* (KM407541), demonstrating the unreliability of this morphotype for species identification. Even the *L. dentatum* lectotype bears irregular branches (Figure 3G) instead of lamellae. Molecular analyses have shown that large morphological variations occur in the same species of *Lithophyllum*, for example, *L. incrustans* and *L. byssoides* (Hernández-Kantún et al. 2015; Pezzolesi et al. 2017). Species of the *L.* '*dentatum*' complex include foliose, encrusting (GDA 61353 and GDA 61377) and lumpy to fruticose (GDA 73872 and GDA 73873) forms. Diverse morphologies linked with sequence data make these particular *Lithophyllum* species good candidates for studying factors influencing morphological plasticity in non-geniculate coralline algae.

Among the Mediterranean *Lithophyllum*, our specimens most closely resemble *Lithophyllum racemus* (Lamarck) Foslie and its cryptic sister species, *Lithophyllum pseudoracemus* Caragnano, Rodondi & Rindi (Caragnano et al. 2020). In addition to the phylogenetic distance, both latter species have only been documented as rhodoliths and differ in tetrasporangial chamber shape (subspherical to nearly spherical) from our specimens (bean-shaped). *Lithophyllum polycephalum* Foslie from blanquizales of the Canary Islands represents the closest morphological and ecological similarity to our specimens, but no molecular data is available for comparison (Afonso-Carrillo 1983, 2021). The only other protuberant species of *Lithophyllum* reported in shallow environments of the Mediterranean is the fruticose *Lithophyllum byssoides* (Lamarck) Foslie found in intertidal areas (Templado et al. 2012; Pezzolesi et al. 2017). Like *L. dentatum*, there are no type sequences available for *L. byssoides*, and the phylogenetic data results in a species complex (Pezzolesi et al. 2017).

The protuberant *Lithophyllum* sp. reported here is currently only known from a narrow subtidal depth range in southern Spain, largely due to the scarcity of taxonomic information of Mediterranean blanquizales. The factors leading to its abundance in this environment is unknown but once established, its thick thallus and protuberances seem suited to blanquizales. Tissue removal by urchins would not reach the basal filaments to allow recovery, while protuberances reduce surface contact and conceptacle exposure (Steneck 1986). The absence of deeper excavating herbivores, like parrotfish in the tropics, should facilitate its persistence.

4.1 | Implications for Conservation

Halting and preventing biodiversity loss is a huge task, and one of the obstacles is the lack of taxonomic and geographic information (Hochkirch et al. 2021). This study contributes to both aspects. We refrained from naming these protuberant *Lithophyllum* sp., but sequence data suggest that it (PQ593847) is the same species as foliose specimens (KM407539, KR708613) distributed along the Mediterranean coast of Spain. It is unknown whether transitions between the two morphotypes can occur depending on the environmental conditions. In the Mediterranean, this protuberant *Lithophyllum* sp. is known only from a narrow depth range in semi-protected rocky settings along the southern coast of Spain. It might have conservation value as its presence fosters higher diversity than typical blanquizales by providing more complex three-dimensional structures for colonization. Fleshy and geniculate algae were denser in these areas, perhaps afforded protection from grazing by the uneven surfaces of the thallus (Afonso-Carrillo 2021). However, urchins were also observed in greater numbers residing in the spaces of the macrostructure of the protuberant *Lithophyllum*, probably feeding on algal overgrowth that becomes accessible. Microhabitats in the thallus also hosted filamentous algae and other invertebrates, which similarly benefit from the increased structural complexity available (Afonso-Carrillo 2021). Since typical blanquizales are considered stable environments (Pinna et al. 2020), it is worth investigating if the increased colonization resulting from the presence of protuberant thalli allows for a transition to a more vegetated environment over time.

This study further adds to the reports of cryptic species and morphological plasticity in the genus *Lithophyllum*, emphasizing the importance of genetic data for confirming species identification and distribution. Accurate baseline information is integral to planning and managing conservation initiatives, especially if preservation of genetic and morphological diversity is a desired conservation goal.

Author Contributions

Dino Angelo E. Ramos: investigation, writing – original draft, writing – review and editing, visualization, formal analysis, data curation. **Jesús Del Río:** conceptualization, investigation, writing – review and editing, data curation, resources. **Julio Peñas:** investigation, writing – review and editing, resources. **Juan C. Braga:** conceptualization, investigation, writing – review and editing, formal analysis, supervision, funding acquisition, resources.

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Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Sequences generated by this study are available from GenBank (https://www.ncbi.nlm.nih.gov/genbank/), and images are available from the University of Granada Herbarium where samples were registered.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.