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# A giant thallus of *Ulva fenestrata* documented from Pillar Point, California, USA

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## Abstract

*Ulva fenestrata* (sea lettuce) is a common green macroalga that contributes to coastal ecosystem productivity. We report an exceptionally large *U. fenestrata* specimen collected from Pillar Point, California. Field observations confirmed that the blade was a single continuous thallus exceeding 4 m², among the largest *Ulva* thalli documented. The blade was thin, translucent, perforated, and distromatic. DNA barcoding using 18S rRNA, *rbc*L, and *tuf*A confirmed its identity as *U. fenestrata*. This observation expands the known size range of *U. fenestrata* and highlights its remarkable growth plasticity under favorable natural environmental conditions.

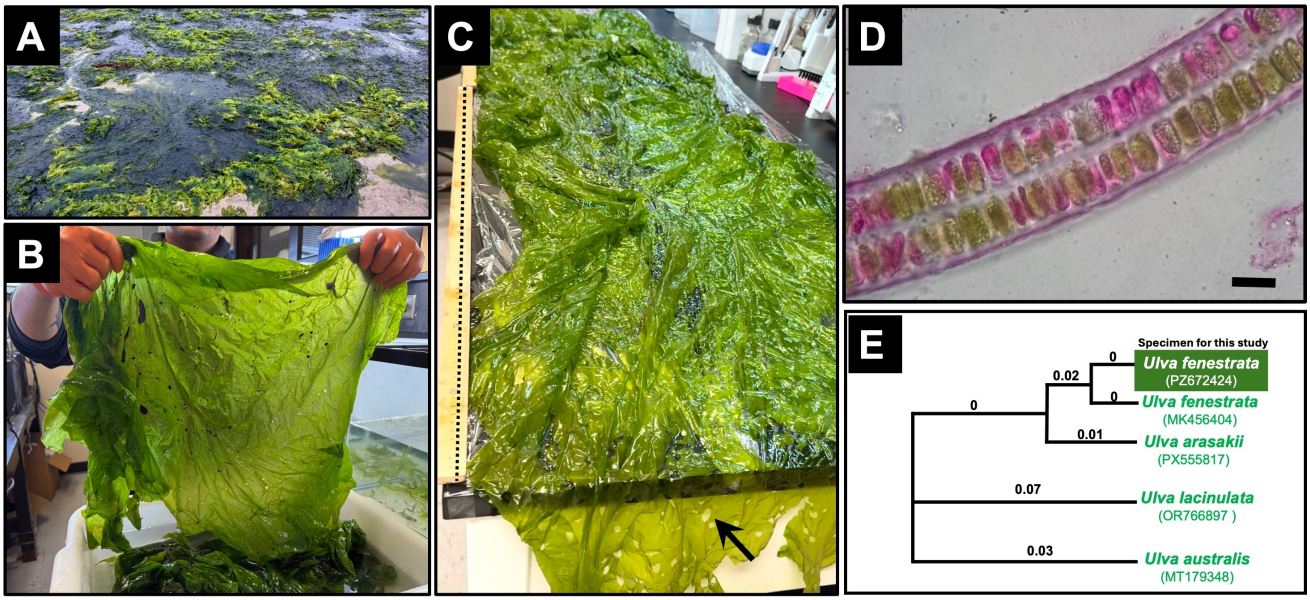



**Figure 1. Identification of an exceptionally large *Ulva fenestrata* thallus from Pillar Point, California:**

**(A)** Field site at Pillar Point, California, where the giant *Ulva* thallus was observed growing on rocks in the intertidal zone (37°29'51.2"N 122°29'44.4"W). **(B)** Portion of the collected thallus held by a researcher, illustrating its thin, translucent blade morphology and exceptional size. **(C)** The thallus spread on a laboratory bench, with a meter stick for scale. The collected material represented only a portion of a single continuous thallus, which was estimated to cover more than 4 m² in total area. The arrow indicates the holes characteristic of *U. fenestrata*. **(D)** Cross-section of the blade showing the characteristic distromatic organization of *Ulva*. Chloroplasts appear green, and the infiltrated Phloxine B appears pinkish-orange. Scale bar = 50 µm. **(E)** Phylogenetic tree based on *tuf*A sequences, placing the Pillar Point specimen (Specimen for this study) within *Ulva fenestrata* and distinguishing it from several other common *Ulva* species. GenBank accession numbers are listed underneath each species name.

## Description

*Ulva* is a globally distributed genus of green macroalgae found in marine, estuarine, and freshwater habitats (Xie et al. 2020). *Ulva* species are ecologically important primary producers and are widely used as food, feed, and sources of bioactive compounds for agricultural and biotechnological applications (Bolton et al. 2016). The genus exhibits remarkable morphological diversity, encompassing filamentous, tubular, and blade-forming growth forms, and currently includes nearly 100 recognized species (Guiry and Guiry 2026). Morphological identification of *Ulva* is often challenging because thallus shape can vary substantially among species and within a species in response to environmental conditions

(Steinhagen et al. 2019; Liu et al. 2020). For example, *Ulva compressa* can develop either free-floating blade-like thalli or attached tubular morphologies depending on habitat characteristics (Steinhagen et al. 2019). This pronounced phenotypic plasticity reflects the capacity of *Ulva* species to respond to local microbial and environmental conditions, and may contribute to substantial variation in growth and size (Teichberg et al., 2010).

An unusually large *Ulva* specimen was discovered in the intertidal zone at Pillar Point, California (Figure 1A). Field observations confirmed that the specimen consisted of a single continuous thallus rather than multiple overlapping blades. Although only a portion of the thallus was collected, direct observations indicated that the intact blade exceeded 4 $m^2$ in area. The thallus was light green, highly translucent, and perforated by numerous small holes distributed throughout the blade (Figure 1B, C).

To characterize the specimen anatomically, blade sections were stained with Phloxine B following vacuum infiltration and examined using brightfield microscopy. Cryosections revealed a distromatic blade structure composed of two cell layers throughout the thallus (Figure 1D), a characteristic feature of blade-forming *Ulva* species. Cell morphology and tissue organization were consistent with previous descriptions of *U. fenestrata*.

Accurate species identification within the genus *Ulva* is often complicated by extensive morphological plasticity and substantial genetic variation among closely related taxa. In addition, species assignments based on a single-locus DNA sequencing can be problematic (Liu et al. 2020). To obtain robust species identification, we employed a multi-locus DNA barcoding approach targeting the nuclear 18S gene and the chloroplast markers *rbc*L and *tuf*A. These markers evolve at different rates and provide complementary phylogenetic information from independent genomic compartments, thereby increasing taxonomic resolution and confidence. Initial sequence comparisons using the 18S gene and the *rbc*L gene revealed high pairwise genetic identities to several blade-forming *Ulva* species; however, concordant results from the *tuf*A locus found that the *U. fenestrata* sequence from Pillar Point was identical to the holotype specimen of *U. fenestrata*. Phylogenetic reconstruction placed the Pillar Point collection in a clade with the holotype specimen of *U. fenestrata* and clearly separated it from other similar-looking bladed *Ulva species* from central California (Figure 1E).

These findings are noteworthy because *Ulva fenestrata* is typically characterized as growing a few centimeters to 1 meter in length (Vinogradova 1974). The exceptional size of the specimen from Pillar Point substantially exceeds the dimensions typically reported for *U. fenestrata*, highlighting the remarkable growth potential and phenotypic plasticity of this species. The occurrence of a giant thallus in a natural coastal habitat suggests that local environmental conditions may influence blade expansion in *Ulva* (Gao et al. 2016). However, because this study did not measure these conditions, their contribution to the observed morphology remains unknown. This specimen provides a valuable natural example for future investigations into the physiological and biomechanical mechanisms underlying giant thallus development and marine macroalgae responses to changing coastal environments.

## Methods

**Seaweed collection and culture**. Fresh *Ulva* specimens were collected from the intertidal zone at Pillar Point, Half Moon Bay, California (37.495° N, 122.498° W) during low tide between June and September 2025. The sample shown in Figure 1 was collected at 9:00 am PST on June 16, 2025. Samples were transported to San Francisco State University and submerged in seawater collected from the sampling site. Upon arrival, specimens were maintained in aerated aquaria containing artificial seawater (~35 ppt Instant Ocean) supplemented with Guillard's F/2 medium (Guillard 1975). Cultures were maintained at 14°C under a 16 h light/8 h dark photoperiod. The collected *Ulva* specimen was pressed, dried, and deposited in the San Francisco State University (SFSU) Herbarium as a permanent voucher specimen (voucher accession number PB0616).

**DNA extraction, PCR amplification, and sequencing.** Seaweed tissue was rinsed with sterile seawater to remove debris and epiphytes, surface-sterilized in 70% ethanol, rinsed again, blotted dry, and flash-frozen in liquid nitrogen. Approximately 100 mg of blade tissue was ground to a fine powder using a mortar and pestle. Because the tough, polysaccharide-rich tissue produced a viscous homogenate, we optimized a direct PCR protocol using Phire Plant Direct PCR Master Mix (Thermo Fisher Scientific, F160S). Approximately 0.8 mg of powdered tissue was homogenized in 20 µL of the supplied dilution buffer using a disposable polypropylene pestle and centrifuged at 20,000 x *g* for 5 min. The resulting supernatant was used as the DNA template. PCR conditions were adjusted to accommodate the physical properties of the algal tissue, and PCR products from the 18S, *rbcL*, and *tufA* loci were obtained for Sanger sequencing and phylogenetic analysis.

Fragments of the nuclear 18S rRNA gene and the chloroplast *rbc*L and *tuf*A loci were amplified by PCR using primer pairs For the 18S gene, these two primers, 5'-CAGCAGCCGCGGTAATTCC-3' (18S-566F) and 5'-CCCGTGTTGAGTCAAATTAAGC-3' (18S-1200R) were used (Hadziavdic et al., 2014). The chloroplast *tufA* gene was amplified using the primers tufGF4 (forward: 5′-GGNGCNGCNCAAATGGAYGG-3′) and tufAR (reverse: 5′-CCTTCNCGAATMGCRAAWCGC-3′), as described by Saunders and Kucera (2010). The chloroplast *rbcL* gene was amplified using the primers GrbcLnF (forward: 5′-GCTGGWGTAAAAGATTAYCG-3′) and GrbcLR (reverse: 5′-TCACGCCAACGCATRAASGG-3′) (Saunders and Kucera 2010). PCR reactions were performed using Phire Plant

Direct PCR Master Mix according to the manufacturer's instructions in an Applied Biosystems GeneAmp PCR System 9700 thermocycler. Cycling conditions consisted of an initial denaturation at 95°C for 5 min, followed by 30 cycles of 93°C for 1 min, 45°C for 30 s, and 72°C for 2 min, with a final extension at 72°C for 7 min. For the *rbc*L primers, the annealing was at 54 °C for 45 s.

PCR products were visualized on 2% agarose gels and purified using the QIAquick PCR Purification Kit (Qiagen) according to the manufacturer's protocol. Purified amplicons were submitted to Elim Biopharm (Hayward, CA, USA) for Sanger sequencing. Sequence assembly and editing were performed using Geneious Prime (version 11.1.5). Consensus sequences were compared against reference sequences available in GenBank using BLAST. Phylogenetic analyses were conducted using Geneious Prime's Neighbor-Joining Tree Build Method with Jukes-Cantor Genetic Distance Model. Newly generated *tuf*A, 18S, and *rbc*L sequences have been deposited in GenBank under accession numbers PZ672424, QB220652, and QB223668, respectively.

**Cryosectioning and microscopy.** For anatomical characterization, blade tissue was stained with Phloxine B and vacuum-infiltrated to improve dye penetration. Tissue samples were embedded in Optimal Cutting Temperature (OCT) compound (Fisher Scientific), frozen in a dry ice–ethanol bath, and sectioned at 30 µm thickness using a Leica CM1850 cryostat. Sections were mounted on glass microscope slides and imaged using brightfield microscopy. Images were acquired using a Nikon Eclipse 80i microscope. Brightfield images were collected at 40X magnification and saved as TIFF files using QCapture Pro software.

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