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Tropical seagrasses reached Patagonia during Miocene times

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We report unequivocal evidence of seagrasses preserved in radiometrically constrained sediments (20.5 Ma) from Patagonia (Gaiman Formation), substantially extending their known palaeogeographic distribution. The new morphospecies *Thalassotaenia notophyllum* sp. nov. was erected based on well-preserved leaf blades that exhibit characters phylogenetically close to the genus *Thalassia* (Hydrocharitaceae), today distributed predominantly in tropical regions. Exquisitely preserved epibionts—diatoms, bryozoans, polychaetes, and coralline algae—occurred on these Miocene leaves, indicating that seagrass-dominated ecosystems were well established at high South American latitudes. Our finding implies that average sea surface temperatures in Patagonian coastal waters during the early Miocene were substantially warmer than today. The warm conditions are also supported by the presence of marine and terrestrial palynomorphs recovered from the seagrass-bearing sediments. Since seagrass ecosystems rank amongst the most important natural carbon sinks on earth, our discovery from Patagonia provides evidence that the wider past extension of seagrasses may have had a more important role in the Cenozoic carbon cycle than previously thought.

Seagrasses are submerged flowering plants growing nearly worldwide in shallow and wave-sheltered marine habitats. Their colonization in the marine realm represents a substantial adaptive challenge, including, for example, tolerance to submergence and salinity, the development of specialized mechanisms for underwater pollination (hydrophily), dispersion of disseminules (hydrochory), and robust vegetative anchorage¹. Seagrasses are among the few plants that have secondarily evolved these ecological adaptations, accounting for only 0.02% of the approximately 300,000 currently described angiosperm species¹. They are represented by six different monocotyledonous plant families within the order Alismatales, including Zosteraceae, Cymodoceaceae, Posidoniaceae, and Hydrocharitaceae^{1–4}. Since their first appearance in the Cretaceous^{5,6}, seagrass meadows have played a critical role by providing habitat and nursery grounds for a wide variety of marine organisms (e.g., fish, crustaceans, bryozoans, and mollusks). They are also highly effective at sequestering carbon dioxide by capturing and storing carbon in their biomass and around the sediment where they grow, making them important in mitigating climate change⁷. However, seagrasses are particularly rare in the fossil record because of their low preservation potential (e.g., virtual absence of lignin and reduced sporopollenin within pollen exines). Most of the past distribution of seagrasses has been commonly reconstructed based on the presence of other proxies better represented in the record, either biological, such as

ostracods^{8,9}, sirenians^{10,11}, bryozoans¹², and foraminifera¹³, or sedimentological, such as seagrass-related carbonate ramps¹⁴.

Here, we report fossil leaves attributable to seagrass species from Lower Miocene sediments of the Gaiman Formation (Chubut province, northeastern Patagonia, Argentina) for which radiometric ages have been recently obtained¹⁵. We use a phylogenetic analysis to assess the relationship of these fossils to all living seagrass members. We also quantitatively estimated marine conditions (i.e., sea surface temperature (SST), sea surface salinity (SSS), and Carbon phytoplankton biomass) using the bioclimatic profiles of the fossils' nearest living relatives. The preserved terrestrial components (i.e., fossil spores and pollen grains) from the leaf-bearing beds were also analyzed to reconstruct the surrounding terrestrial plant communities. Our Patagonian record represents the southernmost fossil record of tropical seagrasses assigned to Hydrocharitaceae. Previous biogeographic hypotheses—including mostly northern hemisphere routes of dispersals—should be revised after this novel discovery.

Geological setting

The studied samples/materials come from the Lower Miocene Gaiman Formation (GF) cropping out at Isla Escondida (northeast Chubut province, Argentina) (Fig. 1a). The GF represents a land-sea transition to inner shelf depositional settings. It was accumulated during the 'Patagoniense', a

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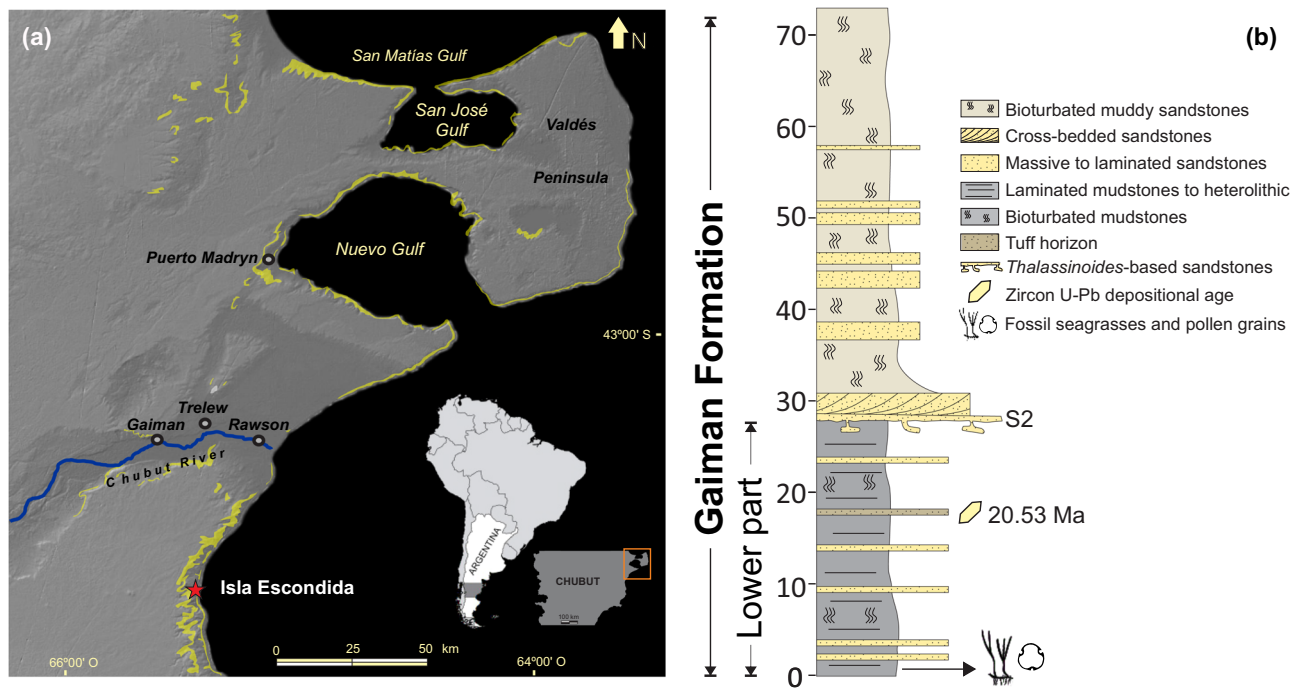


Fig. 1 | Location map and stratigraphic section of the Gaiman Formation (northeastern Patagonia). **a** Geographic position of the analyzed fossil samples. **b** Stratigraphic section cropping out at Isla Escondida locality. Fossil leaves and palynomorphs come from the same level. S2: regional stratigraphic surface

separating the lower (coastal deposits) and upper (shoreface and inner shelf deposits). See further information on the sedimentological cycles in Supplementary Notes 4.

regional episode of marine sedimentation during the Early Miocene in eastern Patagonia¹⁶. The GF includes bioturbated mudstones and muddy sandstones, rich in tuffaceous sediments, as well as minor laminated or cross-bedded sandstones. Fossil invertebrates are poorly preserved, with large oysters as the most common elements¹⁵. Marine vertebrates are abundant and usually well-preserved, including cetaceans^{17–24}, fish²⁵, turtles²⁶, and penguins²⁷. Microfossils are generally scarce, except for diatoms²⁸. The plant-bearing horizon lies at the lowermost part of the coastal cliff exposed at Isla Escondida (Fig. 1a), being part of the lower beds of the GF¹⁵. The horizon includes faintly laminated siltstones with some syn-sedimentary deformational structures. The whitish color of the sediments is probably due to the high input of volcanic ash (Fig. 1b). The overlying ~30 m of sediments include massive laminated, or heterolithic tuffaceous siltstones, very fine sandstones, and tuff, which are occasionally bioturbated and contain some molds of fossil mollusks, indicating a coastal marine depositional environment. Upward in the stratigraphic section, the regional surface S2 delineates the boundary between these coastal deposits and the overlying shoreface and inner shelf deposits, suggesting a transgressive depositional succession¹⁵. Seventeen meters above the plant-bearing horizon, a tuff bed was dated at 20.53 ± 0.46 Ma (latest Aquitanian-earliest Burdigalian) through the zircon U-Pb method¹⁵.

Results

Systematic Paleontology

Family Hydrocharitaceae Juss.

Fossil genus: *Thalassotaenia* van der Ham et van Konijnenburg-van Cittert

Type species: *Thalassotaenia debeyi* van der Ham et van Konijnenburg-van Cittert

Comments on the genus: The morphological traits observed in the Miocene leaves from Patagonia are shared by other fossil morphogenera from the Northern Hemisphere. *Thalassotaenia* van der Ham et van Konijnenburg-van Cittert²⁹ is a morphogenus that encompasses detached, strap-shaped leaves with parallel, longitudinal veins, cross veins, and a prominent central vein²⁹. The fossil leaves in our collection conform well to

this diagnostic description. Subsequently, Benzecry & Barck-Hanes³⁰ proposed the genus *Thalassites*, which includes both leaves and rhizome systems, with leaf venation patterns resembling *Thalassotaenia*. In this study, we assign our material to *Thalassotaenia*, following the principle of nomenclatural priority, and because no organically connected rhizomes were associated with the fossil leaves.

Thalassotaenia notophyllum Panti sp. nov.

Diagnosis: Strap-shaped leaves, thin and very narrow, width ranging between 1.3 mm and 4.7 mm, eligulate, parallel-veined with perpendicular and, rarely oblique, cross veins, and a prominent middle vein; with fibrous basal sheath, and entire margins. Abundant elongated or circular tannin bars.

Etymology: From the Greek terms ‘noto’, meaning ‘south’, which refers to the geographical area where the fossil was discovered, and ‘phylon’, meaning leaf.

Holotype: MPEF-Pb 13603

Paratype: MPEF-Pb 13604–13623

Repository: Museo Paleontológico Egidio Feruglio (MEF), Trelew, Argentina (repository acronym MPEF-Pb).

Type locality: Isla Escondida, Gaiman Fm., Chubut province, northeastern Patagonia, Argentina.

Age: Early Miocene.

Description: The most abundant remains are elongated leaves, strap-like in shape (Fig. 2a), some falcate (Fig. 2b), up to 50 mm long (the longest recorded remains) and 1.3–4.7 mm wide, eligulate (i.e., without a tongue-like structure produced as an adaxial outgrowth at the junction of sheath and blade), with entire margins. No leaf apices have been recognized. Leaf venation is parallel, with 10–18 longitudinal veins, and transversal and (occasionally) oblique cross veins (Fig. 2c, d). The midvein is prominent, and the two marginal veins on each side are also conspicuous (Fig. 2c). Tannin bars are abundant, elongated, or circular in outline (Fig. 2e, f).

Comments: We found a few poorly preserved plagiotropic rhizomes along with the leaves, although not organically connected. These rhizomes

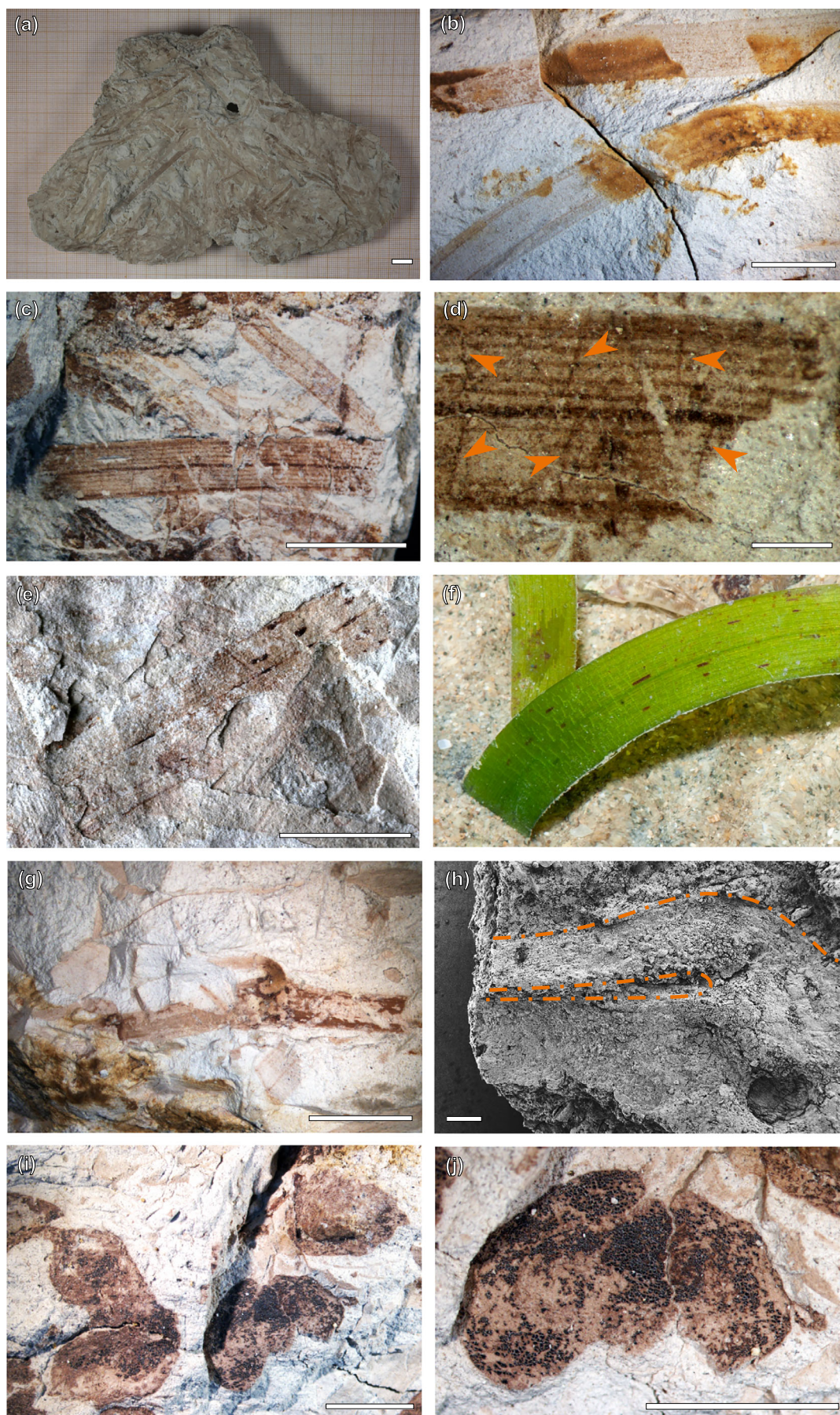


Fig. 2 | Leaves, stems and possible fruits of *Thalassotaenia notophyllum*.

a General view of how fossil leaves are preserved, MPEF-Pb 13604. Scale bar = 105 mm. **b** Strap and falcate leaf shape, MPEF-Pb 13605. Scale bar = 5 mm. The orange color that appears around vascular bundles probably provided a scaffold for mineral (especially iron) deposition. **c** Leaf impression showing the parallel venation and more prominent mid and marginal veins, MPEF-Pb 13603. Scale bar = 5 mm. **d** Detail of leaf showing the parallel venation and the cross veins (orange arrows),

MPEF-Pb 13603. Scale bar = 1 mm. **e** Fossil leaf with elongated tannin bars, MPEF-Pb 13606. Scale bar = 5 mm. **f** Extant sickle seagrass leaf (*Thalassia hemprichii*) showing elongated tannin bars. Photo credit: Ria Tan. **g** Plagiotrophic rhizome of *Thalassotaenia notophyllum*, MPEF-Pb 13607. Scale bar = 5 mm. **h** SEM detail of the rhizome showing the insertion of the root, MPEF-Pb 13608. Scale bar = 300 μ m. **i, j** Possible fruits of *Thalassotaenia notophyllum*, MPEF-Pb 13609. Scale bar = 5 mm.

range from 1.7 to 2.3 mm in diameter and exhibit apparent annular scars at the nodes separated by internodes of ~ 7 mm in length. Each node bears at least one short root (Fig. 2g, h). No leaf scars were observed. These specimens differ from the stem morphogenus *Thalassiocharis* Debey ex Miquel due to its unique striated surface pattern^{31,32}. The stem of the species *Thalassites parkavonensis* Benzecry & Brack-Hanes exhibits broad morphological similarities, including a comparable overall shape and the presence of plagiotrophic rhizomes with unbranched roots³⁰; however, it differs in being larger and in having connected leaves with stomata. Possible fruits, oval to semi-circular in outline with a rugose surface texture, were associated with the leaves and rhizomes. These fruits measure 7.5 mm in length and 4.7 mm in width, and feature a peduncle and a beak at the apex (Fig. 2i, j). They show broad similarities with those of extant *Thalassia* Banks ex K.D. Koenig, but they are smaller and might represent the early developmental stages of the fruits.

Comparisons: Fossil leaves assigned to seagrasses have been primarily attributed to extant genera, often based on vague descriptions (Tables S1, S2). Only a limited number of formal diagnoses of fossil morphotaxa are available. Among these, *Thalassotaenia debeyi* van der Ham & van Konijnenburg-van Cittert, described from the Maastrichtian of Belgium, Netherlands, and Germany²⁹, shares with our material the presence of a strap-shaped leaf, a similar number of parallel veins connected by cross veins, and prominent mid- and marginal veins, but differs in having considerably wider leaves. Other key epidermal anatomical details are not preserved in the Patagonian fossils, precluding more in-depth comparisons. Specimens from the Early Maastrichtian of Tennessee (United States)³³ are comparable but differ in being ligulate. *Thalassodendron auricula-leporis* den Hartog, *Cymodocea floridana* den Hartog, “*Cymodocea*” sp., and “*Halodule*” sp. from the Eocene of Florida (United States)^{30,34} differ in being ligulate (the former three) or having only one central vein (the remaining one). Fossil specimens referred to extant *Thalassia testudinum* Banks & Sol. ex K.D. Koenig, also from the Eocene of Florida³⁴—where they grow nowadays—are morphologically related to the Patagonian specimens but slightly wider. *Thalassites parkavonensis* from the Eocene of Florida, which includes organically connected leaves and stems, differs from our material in having stomata and wider leaves arranged in terminal clusters³⁰. Fossils referring to extant *Cymodocea* K.D. Koenig, like *C. michelotti* Laurent & Laurent from the Miocene of Sulawesi³⁵ and *C. cf. nodosa* Asch. from the Miocene of Spain³⁶, differs by being ligulate. Other specimens from the same locality were assigned to extant Alismatales *sensu lato*, although the poor preservation hindered accurate comparisons³⁶. Miocene-Pliocene seagrass fossils from the South Island, New Zealand, with apparently revolute leaf margins, suggest affinities with the present-day tropical to subtropical Hydrocharitaceae genus *Enhalus*^{37,38}. These fossils were not formally described and are under ongoing research.

Phylogenetic analysis: We found a close morphological relationship with seagrasses of the Hydrocharitaceae, particularly with *Thalassia*,

Enhalus Rich., and *Halophila* Thouars. While *Halophila* is characterized by paddle-shaped or fern-like leaves, both *Thalassia* and *Enhalus* are distinguished by strap-shaped leaves with parallel venation, closely resembling the fossil specimens from Patagonia. However, *Enhalus* possesses much wider and revolute-margined leaves. A backbone constraint phylogenetic analysis using 23 morphological characters supports our taxonomic assignment, placing the fossils as sister to the living genus *Thalassia* (Fig. S3 and Table S2).

Paleoecological context: the flattened blades of *T. notophyllum* hosted diverse epibiont communities including epiphytic coralline algae, diatoms (e.g., *Cocconeis* sp.), encrusting euryhaline bryozoans (e.g., *Electra* sp., *Membranipora* sp.), and *Spirorbis* (Fig. 3). According to the bioclimatic profiles of *T. notophyllum* nearest living relatives, the sea conditions may have been markedly different from those of today along the northeastern Patagonian coast. For example, the reconstructed scenario suggests much warmer sea surface temperatures ($>25^{\circ}\text{C}$), higher sea surface salinity (~ 34 – 36 ppm), and lower carbon phytoplankton biomass (0.5 – $1.5 \mu\text{M}/\text{m}^3$) (Figs. 4–5). The palynological assemblage recovered from the seagrass-bearing sediments, with abundant terrestrial and fewer marine elements, indicates the presence of a shallow subtidal estuarine environment (Notes S2, Table S3). The high relative proportion of prasinophytes and acritarchs compared to dinocysts indicates stratified water column conditions very close to the coastline^{39,40}. The terrestrial-derived spores and pollen grains suggest that a salt-stressed plant community developed near the coastline. The main preserved elements include chenopods (Amaranthaceae), alkali-weeds (*Cressa*, Convolvulaceae), joint-pines (*Ephedra* L., Ephedraceae), and Calyceracean taxa. The palynological assemblage also includes palms (Arecaceae), shrubs of the Asteraceae (*Proustia* Lag./*Lophopappus* Rusby), and Araucariaceae trees. In well-drained soils, may have developed legume trees (*Prosopis* L. and *Caesalpinia* L.), and Anacardiaceae (*Schinus* L.), forming semi-deciduous communities. Upstream from the Patagonian coast or in mainland areas, humid-demanding forests dominated by abundant podocarps (e.g., *Podocarpus* Labill., *Dacrycarpus* (Endl.) de Laub., *Dacrydium* Lamb., *Lagarostrobos* Quinn) and southern beeches (*Nothofagus* Blume) and Proteaceae, along with other wet-demanding taxa such as Winteraceae (*Drimys* Juss.), and ferns (Cyatheaaceae and Dicksoniaceae) occurred (Fig. 6, Figs. S1, S2, Table S3).

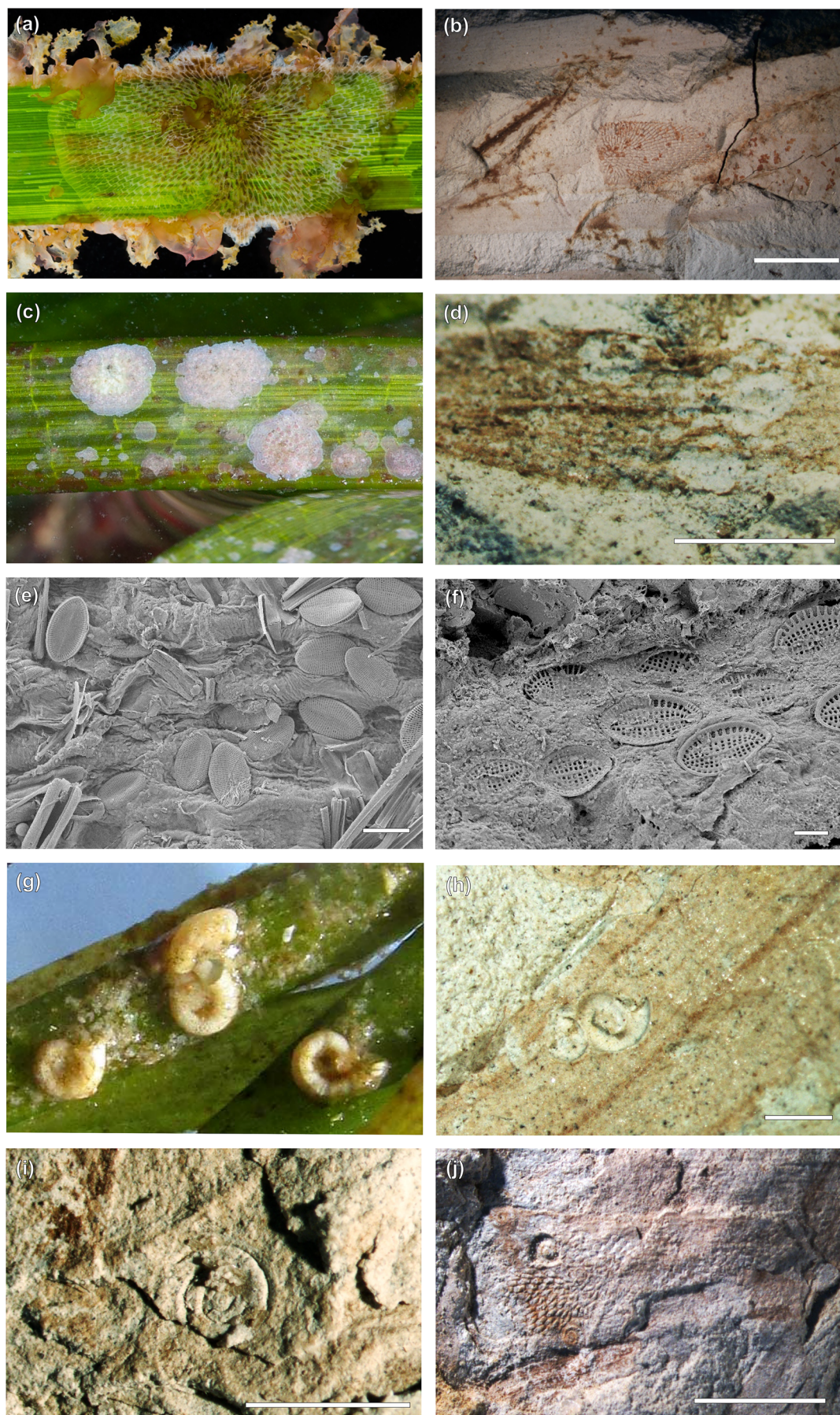
Discussion

The discovery of fossil tropical seagrasses in early Miocene sediments from Patagonia—an area now characterized by much cooler conditions—suggests that the local climate and oceanic environment were markedly different (Fig. 7). Furthermore, our finding is particularly remarkable given the inherent challenges of seagrass preservation (e.g., fragile tissue composition). The early evolution of the Hydrocharitaceae, the angiosperm family most closely related to our fossil specimens, may have occurred in Europe during the Cretaceous, and subsequently dispersed to all continents (except

Fig. 3 | Epibionts from extant seagrasses and fossil *Thalassotaenia notophyllum*.

a Colony of bryozoans (*Membranipora* sp.) attached to an eelgrass leaf (*Zostera marina*). Photo credit: Gustav Paulay. **b** Mold of epiphytic colony of bryozoans attached to fossil leaves, MPEF-Pb 13605. Scale bar = 5 mm. **c** Encrusting coralline red algae on tape grass (*Enhalus acoroides*). Photo credit: Ria Tan. **d** Fossil imprints of probable encrusting red algae on *T. notophyllum*, MPEF-Pb 13612. Scale bar = 5 mm (their presence can only be indirectly inferred due to the lack of cellular

structures). **e** Epiphytic diatoms on living *Thalassia testudinum*. Scale bar = 10 μ m. **f** Epiphytic diatoms found on fossil leaves referred to the genus *Cocconeis* Ehrenberg, MPEF-Pb 13613. Scale bar = 10 μ m. **g** Several *Spirorbis* sp. covered shoal grass leaves (*Halodule wrightii*). Photo credit: Jim Conrad. **h, i** Probable *Spirorbis* attached to the leaves of *Thalassotaenia notophyllum*. **h** MPEF-Pb 13607. Scale bar = 1 mm. **i** MPEF-Pb 13612. Scale bar = 5 mm. **j** Several epibionts coexisting on leaves of *Thalassotaenia notophyllum*, MPEF-Pb 13606. Scale bar = 5 mm.



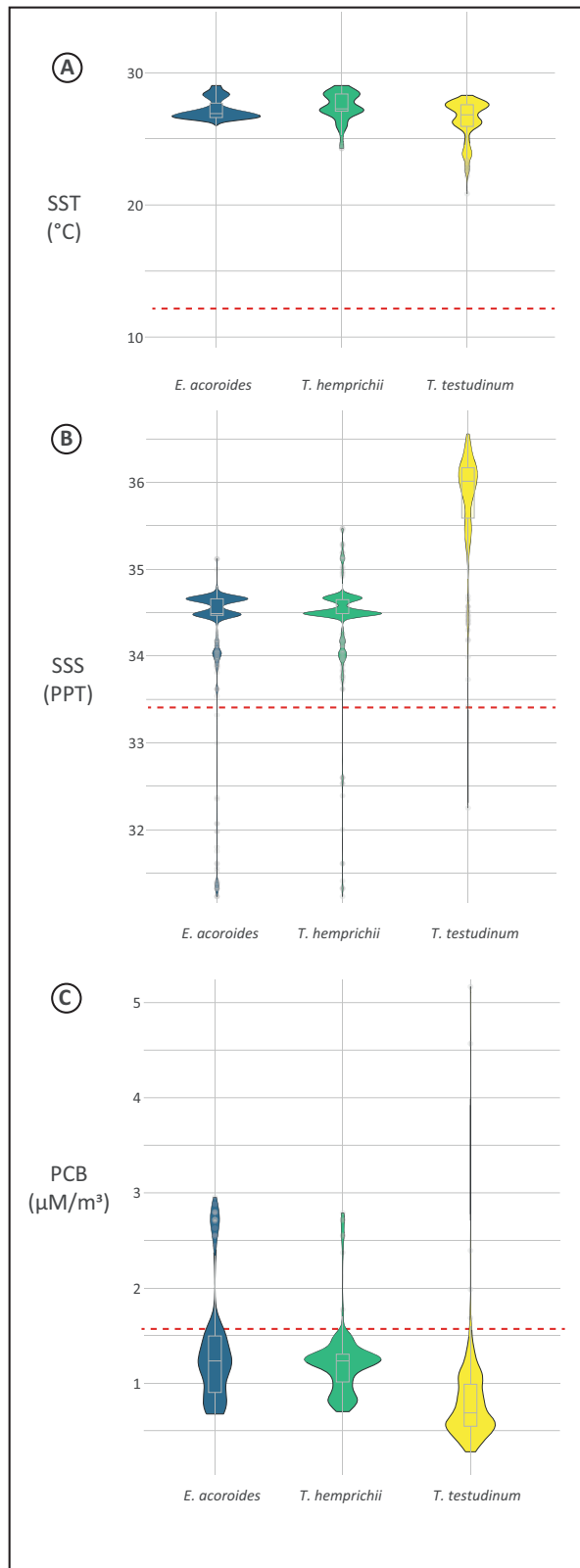


Fig. 4 | Bioclimatic and geophysical profiles of the fossils' nearest living relatives using beanplots. A SST sea surface temperature. **B** SSS sea surface salinity. **C** PCB carbon phytoplankton biomass. Red dashed-lines represent present-day conditions in the northeastern Patagonian coast.

Antarctica) during the Cenozoic according to a recent analysis of Ulrich et al.⁴¹. However, the assumed place of origin of this family seems heavily biased towards the northern hemisphere where most of the fossil records of the family come from⁴¹. The record of other unquestionable seagrasses assigned to Hydrocharitaceae comes from the Eocene of North America^{30,34,42–47}. Our new evidence from southern South American Patagonia supports the notion that the geographic extension of tropical seagrasses was more widespread in the past than previously thought. Other known records assigned to seagrasses of the Hydrocharitaceae (*Enhalus*-like) from the South-West Pacific region come from Miocene-Pliocene sediments of New Zealand^{37,38}. However, the specimens have not yet been formally described. We hypothesize that tropical seagrasses of the Hydrocharitaceae family extended to the southernmost latitudes of Australia, New Zealand, and South America at least during the Neogene. Their current restricted geographic distribution to tropical regions likely results from significant extinction events during the cooling trend of the late Neogene, as evidenced by the limited number of living species (Fig. 5). *Thalassia* appears to have retained its ancestral ecological traits—including climatic tolerances—over evolutionary time. Similarly, many other clades widely distributed in Patagonia during the early Miocene (earlier than the Miocene Climatic Optimum) have never successfully returned to these high-latitude regions (e.g., palms, platyrrhine monkeys)^{48,49}. The tropical conservatism hypothesis suggests that dispersal into temperate regions has not been prevented by either lack of time or limited dispersal ability, but instead by niche conservatism⁵⁰. In this context, we recovered other warmth-adapted species that disappeared from Patagonia during the late Neogene, as evidenced by the palynological assemblage, including marine dinoflagellate cysts. For example, we recovered *Tuberculodinium vancampoae* (Rossignol) Wall, the resting cyst of *Pyrophacus steinii* (Schiller) Wall & Dale, which blooms under mean sea surface temperatures >25 °C^{51,52}. Interestingly, the sea surface temperatures estimated by modeling studies for the Miocene at these high latitudes⁵³ are much lower (~15–18 °C) than the ones inferred in this study (>25 °C). Additional empirical estimates of past sea surface temperatures from the Patagonian coast are needed to help reconcile the apparent discrepancies.

The preserved epibionts on seagrass blades, including diatoms, coral-line algae, and bryozoans, serve as an excellent proxy for the diversity of this ecosystem. This dense marine meadow was probably used by many other marine invertebrate and vertebrate species for nursery and foraging grounds, including marine fish, marine mammals, shorebirds, and elasmobranchs, many of which have been preserved in the seagrass-bearing sediments^{25,54,55}. Moreover, the large quantity of spores and pollen grains delivered by winds and rivers to the sea reveals that the surrounding floras include palms (Arecaceae), tree ferns (*Lophosoria* C. Presl or *Dicksoniaceae*), and many other plant species that no longer grow in the Patagonian steppe.

Today, seagrass blades and rhizomes host calcareous algae (e.g., coralline red algae), foraminifera, bryozoans, and serpulid worms that secrete calcium carbonate, contributing to carbonate sediment production. For example, the tons of early Miocene sediments from western Australia preserve carbonate platforms produced by temperate to subtropical seagrass meadows (e.g., Haig et al.¹³). The absence of carbonate remains in the seagrass-bearing sediments of the Gaiman Formation may be either because these were dissolved⁵⁶ or because the depositional environment was dominated by tuffaceous volcanic material rather than a carbonate-rich setting¹⁵.

The fossil seagrasses recovered from Patagonia are represented exclusively by non-oriented blades (lacking bases and apices) and a few rhizomes. This suggests that the fossils may not have accumulated in situ, but rather were transported and rapidly deposited by a storm or similar weather event from a nearby location. This interpretation is supported by the preservation of the specimens and the condition of associated

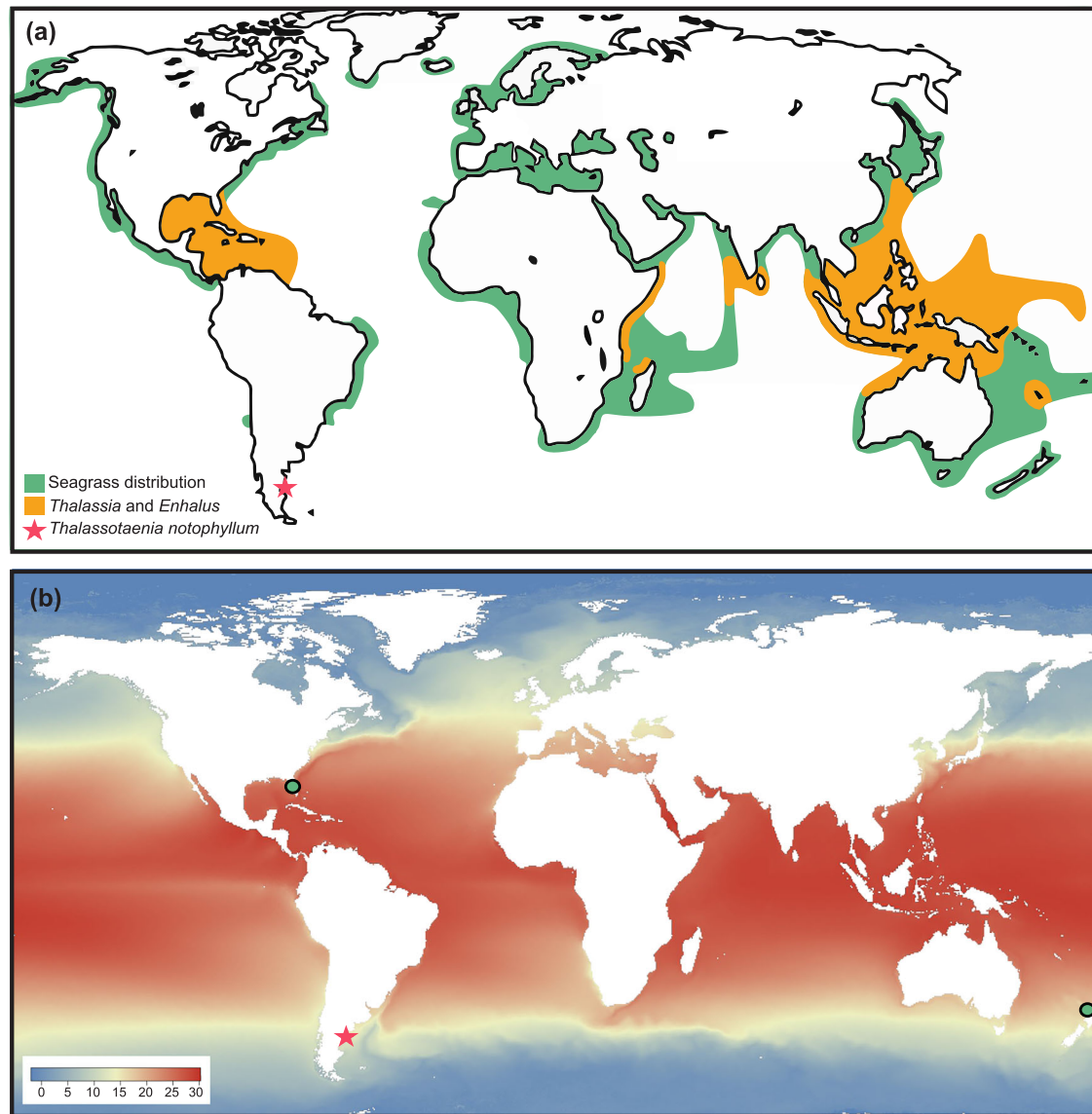


Fig. 5 | Past and present distribution of seagrasses. **a** Present-day distribution of seagrasses, including members of several families within the Alismatales (green-shaded). Tropical seagrass genera *Thalassia* and *Enhalus* of the Hydrocharitaceae (orange-shaded) represent the fossils' nearest living relatives. (Modified from Reich et al.⁸). Note that the Miocene Patagonian specimens (red star) represent the

southernmost record of seagrasses (see Fig. S4 for other seagrass fossil records from the Southern Hemisphere). **b** Green circles represent other tropical seagrass fossil records assigned to Hydrocharitaceae from the Eocene of Florida^{30,34,42–47} and Miocene-Pliocene from New Zealand^{37,38}.

epibionts, indicating minimal transport distance and limited mechanical disturbance.

Overall, the presence of seagrasses in the Miocene from Patagonia suggests that what is now a temperate or cold-temperate ecosystem once supported a rich, warm-water marine habitat with different community dynamics, trophic structures, and biodiversity patterns.

Materials and methods

The fossil samples were recovered by JIC and others from beds cropping out at the Isla Escondida locality, Northeast Chubut Province, Argentine Patagonia (Fig. 1).

Paleobotany

Megafossils were preserved as impressions (shallow imprints) and compressions (flattened imprints that retain some organic material). The material was photographed under unilateral low-angle light with a Nikon DS-Fi1-U2 digital camera is attached to a Nikon SMZ800 stereomicroscope.

Because each sample rock contains several specimens, we temporarily assigned a number to single rock samples. Specimens best preserved were measured and described. Those suspected of bearing organic preservation were soaked in nitric acid (75%). For detailed illustration and analysis, cuticle remains, along with selected fragments of leaves and pollen, were mounted for SEM observation and sputter-coated with gold-palladium (40%–60%) and examined in a scanning electron microscope Zeiss GeminiSEM 360.

Palynology

For palynological purposes, sedimentary samples from two levels were processed using standard palynological techniques⁵⁷, resulting in one fertile sample. Palynomorphs were analyzed and counted using a Leica 2500 microscope. SEM photomicrographs were taken at the Zeiss Gemini scanning electron microscope 360, at the Museo Argentino de Ciencias Naturales. Slides are housed at the Museo Egidio Feruglio, prefixed MEF PA., under catalog number 1571. Fossil spores and pollen grains were

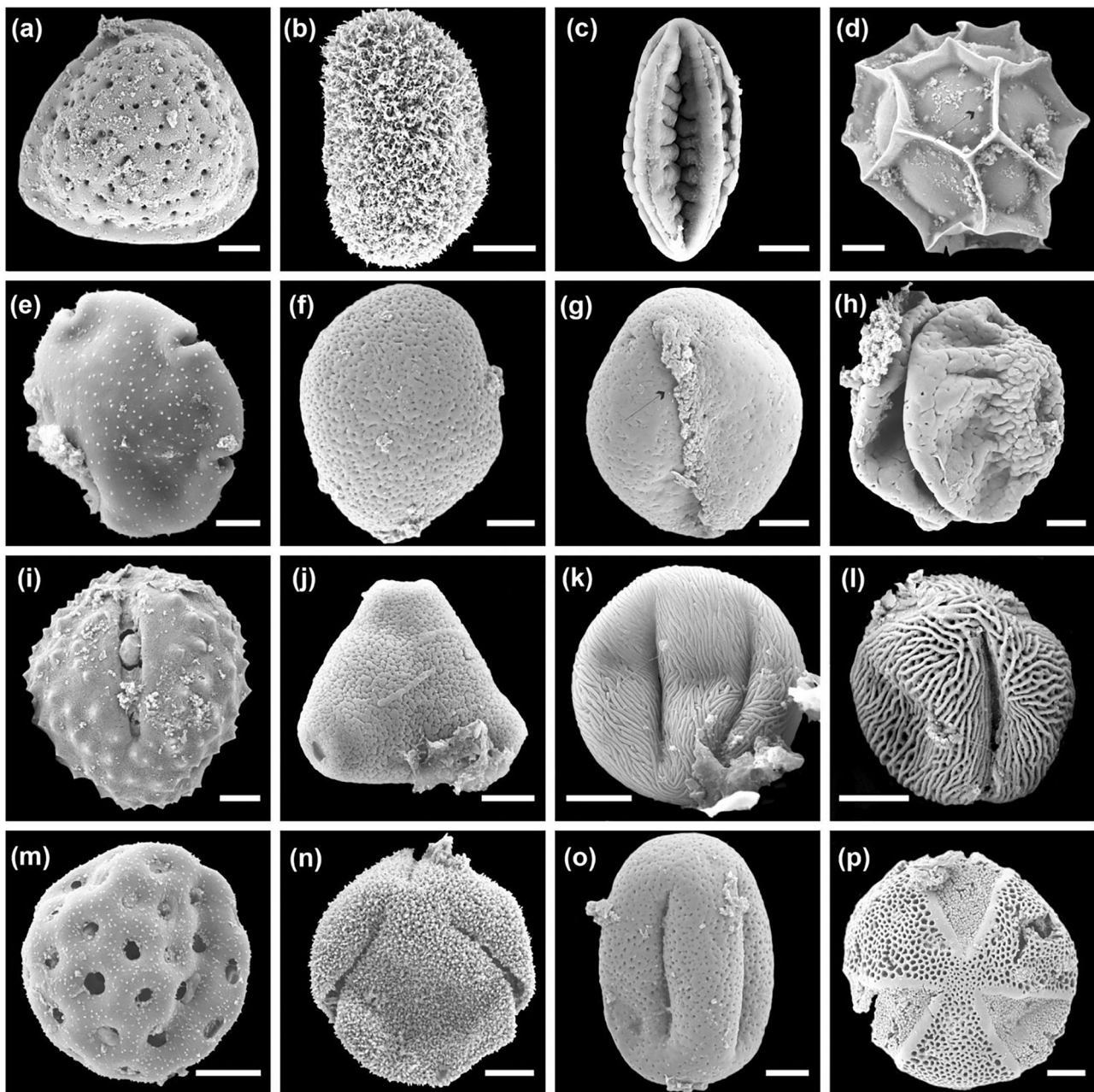


Fig. 6 | SEM images of selected spores and pollen grains from the megafossil-bearing bed of the Gaiman Formation. a *Cyatheacidites annulatus*. **b** *Peromonolites vellosus*. **c** *Equisetosporites claricristatus*. **d** *Cymathiosphaera* sp. **e** *Nothofagidites saraensis*. **f, g** *Arecipites* cf. *otagoensis*. **h** *Dryptopollenites* sp. **i** *Mutisiapollis viteauensis*. **j** *Proteacidites* sp. 1. **k** *Striatricolporites* sp. 2.

l *Striatricolporites* sp. 1. **m** *Chenopodipollis chenopodiaceoides*. **n** *Senipites* sp. **o** *Rhoipites* sp. 2. **p** *Margocolporites vanwijhei*. Scale bar equals 5 μ m, except in figures (a), (b), and (p), where scale bar equals 10 μ m. LM images from specimens of Figs. (a), (f), (h), (i), (n), and (p) in Fig. S1.

identified at the species level whenever possible. We explored the modern botanical affinity of fossil morphotypes and grouped them into taxonomic categories (i.e., families or genera). All palynomorphs were counted, summing a total of 837 counted specimens (Table S3).

Comparative morphology of extant plants

Herbarium specimens were analyzed using high-resolution photographs from Jstor Global Plant (<https://plants.jstor.org/>), GBIF-Global Biodiversity Information Facility (<https://www.gbif.org/>), and other international virtual herbaria (e.g., The Australasian Virtual Herbarium (<https://chah.gov.au/>)). Images were analyzed at the maximum size to identify micromorphological

characteristics of roots, stems, leaves, and reproductive structures. In addition, sites specialized in monitoring and studying seagrasses were consulted (i.e., <https://www.seagrasswatch.org/>).

Bioclimatic analysis

The climatic and environmental profiles of *Thalassia testudinum*, *T. hemprichii* (Ehrenb. ex Solms) Asch., and *Enhalus acoroides* Rich. ex Chatin were reconstructed using R, ⁵⁸ with the package 'sdmpredictors'⁵⁹. Specific locations of the specimens of each species derive from iDigBio and GBIF (Nov 2024) and were obtained using the R packages *rgbif*⁶⁰ and *ridigbio*⁶¹. We used Bio-ORACLE and MARSPEC datasets that include geophysical

Fig. 7 | Hypothetical reconstruction of the early Miocene shallow marine floor from northeastern Patagonia covered by seagrass meadows along with a marine turtle, interpreted on the basis of fossil record from the Gaiman Formation⁶². This reconstruction was created using MidJourney, an AI-based image generation tool, and further reviewed and modified by the authors to align with the scientific context and accuracy required for this study.



and climatic data layers for ecological modeling. We estimated sea surface salinity (annual mean), sea surface temperature (annual mean), and carbon phytoplankton biomass (mean). Coordinates were obtained from GBIF.

Data availability

The authors declare that all fossil specimens (under numbers 1603–1623) and slide (number 1571) are housed at the Museo “Egidio Feruglio” under the catalog prefixed MPEF Pb and PA, respectively. The datasets used for the analyses are available via Zenodo at <https://zenodo.org/records/15792752>.

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Author contributions

J.L.C. & A.A.M. provided stratigraphic information and samples. V.D.B. performed the palynological assemblage description, captured palynomorph images, and designed the figures illustrating them. C.P. performed the megafossil descriptions, captured images, and designed the figures. L.P. contributed to the statistical analysis and illustrations. C.P., L.P., V.D.B. & S.N. wrote the manuscript with contributions from D.G.G., D.P., J.I.C., & M.J.T. All authors edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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