Early Oligocene kelp holdfasts and stepwise evolution of the kelp ecosystem in the North Pacific

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Abstract

Kelp forests are highly productive and economically important ecosystems worldwide, especially in the North Pacific Ocean. However, current hypotheses for their evolutionary origins are reliant on a scant fossil record. Here, we report fossil hapteral kelp holdfasts from western Washington State, USA, indicating that kelp has existed in the northeastern Pacific Ocean since the earliest Oligocene. This is consistent with the proposed North Pacific origin of kelp associated with global cooling around the Eocene-Oligocene transition. These fossils also support the hypotheses that a hapteral holdfast, rather than a discoid holdfast, is the ancestral state in complex kelps, and suggest that early kelps likely had a flexible rather than a stiff stipe. Early kelps were possibly grazed upon by mammals like desmostylians, but fossil evidence of the complex ecological interactions known from extant kelp forests is lacking. The fossil record further indicates that the present-day, multi-story kelp forest had developed at latest after the mid-Miocene climate optimum. In summary, the fossils signify a stepwise evolution of the kelp ecosystem in the North Pacific, likely driven by changes in the ocean-climate system.

Significance statement

Molecular and morphological studies suggest that kelps – large, marine brown algae – originated around the Eocene-Oligocene transition about 34 million years ago. This paper documents kelp holdfasts from earliest Oligocene strata in Washington State, USA, that provide evidence for these age estimates and the morphology of early kelps. The fossils also highlight the preservational potential of brown algal holdfasts, which likely exceeds that of the soft blades that constitute the hitherto known fossil record of kelps. Reviewing the fossil record in light of the new data supports the view that kelp evolution in the North Pacific was stepwise and driven by climatic changes.

Introduction

Kelps, brown macroalgae of the order Laminariales, are among the largest and fastest-growing benthic marine organisms. These ecologically important primary producers play a central role in structuring nearshore temperate habitats on a global scale (1, 2). The largest kelps, such as *Macrocystis* and *Nereocystis*, often grow in vast, dense stands commonly referred to as kelp forests. These are the most productive ecosystems in the temperate marine realm and sustain a growing billion-dollar industry (3-6). The iconic Northeast Pacific kelp forests are complex, highly stratified ecosystems that provide refuge and sustenance for hundreds of invertebrates, fishes, marine mammals, and seabirds (7-10). Despite their importance, the evolutionary origin of these ecosystems remains controversial due to their exceedingly incomplete fossil record. Fossil kelps are only known from Miocene rocks in southern California [11-14 Ma; (11, 12)], and the oldest sirenians, possible kelp-consumers, in the North Pacific are of similar geologic age (13, 14). Molecular age estimates (15-17) and alternative interpretations of the fossil record (18), however, pointed to Oligocene [~32 Ma] or even Cretaceous [~80 Ma] origins of the Laminariales. Newly discovered early Oligocene [c. 32.1 Ma] brown algal fossils from Washington State, USA, preserve cellular details and provide new insights into the evolutionary history of kelp ecosystems in the northeastern Pacific Ocean.

Early Oligocene holdfasts from western Washington

Twelve permineralized hapteral holdfasts were collected from coastal exposures of the Jansen Creek Member of the Makah Formation along the Strait of Juan de Fuca. The Jansen Creek Member is an olistostrome consisting of early Oligocene sandstone and shallow-marine conglomerate enclosed in deep-marine strata, also of early Oligocene age (19). This is confirmed by the $^{87}Sr/^{86}Sr$-ratio (0.707932, uncertainty $2\delta=0.000006$) of a calcitic pteriomorph bivalve shell to which one holdfast is attached, indicating an age of ca. 32.1 Ma (+0.2/–0.2 Ma).

The holdfasts, up to 51 mm in diameter, are formed by conical masses of haptera originating from a single central axis (Fig. 1). Synchrotron radiation x-ray tomographic microscopy (SRXTM) and natural cross sections show that the central axis is narrow-conical in shape and forms the base of the stipe, which is up to 10 mm in diameter (Fig. 1). Close to where the base of the stipe (not preserved) would have been, the haptera emerge from a lobe- or skirt-like meristematic transition zone that radiates outward and downward for up to 12 mm, often with an initial bulge, and then divide into finger-like structures with a minimum diameter of 0.5 mm (Fig. 2A). Thin-sections reveal that the hapteral tissue has a thin darker outer region, one or two cell layers wide, consisting of small cubic cells here interpreted as the meristoderm, and a lighter inner region, interpreted here as the cortex. Cells in the inner region are several cell layers wide, characterized by elongate, uniformly shaped cells often having thick walls (Fig. 2B). The haptera at the base of the permineralized holdfast shape themselves to the micrometer-scale surface features of the substrate (Fig. 2C).

The holdfasts grew mostly on barnacles (Figs. 2A, C, D) and bivalve shells (Figs. 2D–F), some of which we identified as members of the family Mytilidae (Fig. 2F). Within the mass of haptera, the holdfasts have encased various small bivalves, gastropods (Figs. 2E, G, H), foraminifera, rocks and sediment (Figs. 2H). Oxygen isotope ratios of the overgrown invertebrate shells indicate ambient water temperatures ranging from 15.6 to 16.8°C for a barnacle and 19.9 to 23.0°C for a pteriomorph bivalve (Table 1).

We interpret these holdfasts as belonging to the complex kelps (Laminariales) based on the mode of haptera formation. New haptera grew continuously from the basal region of the stipe, overgrowing previously grown haptera (Fig. 1). This type of hapteral holdfast morphology is unique to Laminariales and very different from the discoidal holdfast of *Cymathere triplicata* and those occurring in the order Fucales (20, 21), including the large southern hemisphere ‘bull kelp’ *Durvillaea* (22).

Implications for kelp origins

The Jansen Creek holdfasts provide the first unequivocal fossil evidence that complex kelps existed by earliest Oligocene [~32 Ma] time. This timing is consistent with current molecular age estimates (16, 17) and earlier interpretations of the fossil record (18), and refutes the hypothesis of a late Cenozoic origin based on the first appearances of present-day, kelp-associated herbivorous invertebrates and mammals (13). Most modern kelp forests include species with a stiffened stipe to support upright growth. This character was considered to have evolved independently at least five times from ancestors with a flexible stipe, and rather late in the evolutionary history of the Laminariales (17). The stipe is not preserved in any of the Jansen Creek fossils; instead, the location where the stipe would originate within the holdfast is mostly an inverted-conical cavity (Fig. 1). This type of preservation may suggest that these Oligocene kelps had a soft stipe, which did not support upright growth. It is also possible, however, that the stipes were stiff, but had become dissevered mechanically (e.g., during a storm) or grazed away by animals.

Earlier studies suggested that a discoidal rather than a hapteral holdfast was the ancestral state in Laminariales (23, 24). More extensive phylogenomic analyses have supported removal of morphologically simple families (Akkesiphycaceae, Chordaceae and Pseudochordaceae) from the complex kelps (Order Laminariales), and that a hapteral holdfast is the ancestral state in this clade (17). The hapteral early Oligocene holdfasts described here support this view. The numerous invertebrate specimens entangled in the Jansen Creek holdfasts (Fig. 2) indicate that already these early kelp holdfasts provided micro-habitats for a diversity of organisms, as do their extant counterparts (25, 26). Furthermore, paleotemperature estimates (~16–23°C) based on the invertebrate shells on which the holdfasts grew indicate that these kelps thrived in temperatures within the tolerance range of extant kelps (27), albeit close to its upper limit. This is consistent with the hypothesis that cooler waters following the Eocene-Oligocene transition [~33.9 Ma] were ideal for the initial kelp radiation (3, 13, 17), but it also indicates that early kelps were relatively tolerant of higher temperatures.

Implications for the evolution of kelp ecosystems

The presence or absence of mammalian and invertebrate herbivores has played a prominent role in the long controversy on the origin and evolution of kelp ecosystems (13, 17, 18, 28). Given their fast growth rates and basal growth strategy, early kelps would have represented a considerable food source (29, 30), and desmostylians have long been considered as prominent early kelp consumers (18, 31). These now extinct hippopotamus-sized marine mammals appeared in the Northeast Pacific in the early Oligocene (32) and would have required a large amount of fleshy algal biomass to sustain themselves (18). Their bone structure and anatomy indicate adaptations for hovering slowly at a preferred depth or walking on the seabed (33), ideal for grazing on kelps. The holdfasts documented here show that kelp was a viable food source in the early Oligocene and provide strong support for the hypothesis of early desmostylians being kelp feeders (18, 31).

The fossils furthermore suggest that early kelp beds had no dramatic evolutionary consequences as they did not sustain the diversity and complexity of modern kelp forests, at least until the mid-Miocene [~14 Ma]. They could have facilitated the radiation of plotopterid seabirds in the eastern Pacific (34), which appeared in the latest Eocene and persisted in the region until the early Miocene [~16 Ma], along with the desmostylians (34, 35) (Fig. 3). It was hypothesized that the extinct, bear-like mammal *Kolponomos,* which appeared in the Northeast Pacific in the early Miocene [~23 Ma], had feeding adaptations similar to those of sea otters (36), and may have been feeding on herbivore sea urchins (28). This association was seen as an early analogue to the present-day, top-down forcing of sea otter consumption of urchins (28). However, there is no conclusive evidence of the presence of kelp-feeding sea urchins, including strongylocentrotids, from Oligocene and Miocene [~32–6 Ma] strata in the Northeast Pacific, or that *Kolponomos* did indeed feed on sea urchins, so this hypothesis remains to be tested.

Large mammalian herbivores such as seaweed-feeding sirenians (e.g., Steller's sea cow) did not appear in the cold Northeast Pacific until the late Miocene (14, 37), and there is no evidence for a radiation of kelp-associated marine invertebrates (13) during the Oligocene and Miocene [~32–6 Ma, Fig. 3]. Instead, the North Pacific appears to have received colonists from adjacent warm-water regions and the cold Southern Hemisphere throughout the Oligocene and most of the Miocene, and it was not until the late Miocene [~12 Ma] that the North Pacific started to export evolutionary novelties and biodiversity (28). Molluscan evidence indicates a gradual temperature increase along the entire North American Pacific coast from the mid-Oligocene to a peak during the mid-Miocene climate optimum [~26–14 Ma, (38, 39)], and it is tempting to speculate that this rise in temperature dampened the evolution of the essentially cold-water kelp ecosystem.

The evolutionary dynamics of kelp beds appears to have changed after the mid-Miocene climate optimum, when seawater temperatures dropped drastically, both globally and locally along the American Pacific coast (38, 39). Deposition of the diatom-rich Monterey Formation in California reflects the upwelling of cold, nutrient-rich waters (11), and precisely this sedimentary formation hosts the large kelp fossil *Julescraneia grandicornis* (12; Figure 3). This is the first fossil evidence for large, canopy-forming kelps that likely created the complex, multi-layered kelp forests known today (13, 21). Seaweed-feeding sirenians appeared in the fossil record shortly afterwards [~10–8 Ma, Fig. 3, (14, 37)], and their anatomy suggests that they could have been feeding on the canopy of the kelp forest (14, 37), while paleoparadoxiid desmostylians may have been grazing on understory algae (33). Only this multi-storied kelp ecosystem might have had the complexity to make the North Pacific Ocean the biodiversity pump that it has been since the late Miocene (28).

Herbivorous, kelp-feeding invertebrates such as strongylocentrotid sea urchins and large-sized haliotid gastropods (abalones) appeared in the fossil record of the North Pacific at the beginning of the Pliocene [~5.3 Ma, (40, 41)], small holdfast-inhabiting gastropod limpets in the Pleistocene [~2.5 Ma, (13)], and sea otters apparently colonized the North Pacific Ocean not earlier than middle Pleistocene (42) [620–670 Ka; Fig. 3]. Hence, the iconic top-down forcing in kelp-dominated ecosystems (kelp-urchin-otter interactions) is indeed a very young ecological phenomenon in terms of geologic timescales, as suggested earlier (17, 37). The Plio-Pleistocene arrival of these organisms in the North Pacific kelp ecosystem coincides with continued global cooling (43), but whether their appearance is indeed temperature-driven remains to be tested. Overall, the Jansen Creek holdfasts and our re-evaluation of the fossil and geological record support the hypothesis of a stepwise evolution of the kelp ecosystem in the Pacific Northwest, driven by changes in the ocean-climate system (17, 28, 37).

Materials and Methods

Fossil repository. The fossils are deposited at the Swedish Museum of Natural History (NRM, Stockholm, Sweden) and the University of California Museum of Paleontology (UCMP, Berkeley, USA) under accession numbers NRM S169277, S126520–126529 and UCMP 201250–51.

Strontium isotopes. A sample for strontium isotope analyses was extracted from the polished surface of the counterpart of a thin section using a handheld microdrill. The strontium isotopic composition was analyzed on an unspiked sample. The sample was weighted into a Teflon vial and dissolved in a mixture of 5 ml HF and HNO3 (3:2) with a PicoTrace© digestion system. This form of digestion may imply that tiny amounts of detrital and/or meteoric material are dissolved as well, and therefore the obtained ratios represent maximum ages. The solution was processed by standard cation-exchange techniques for purification of the Sr fractions. Sr was loaded with 0.5N H3PO4 on pre-conditioned double Re filaments. Measurements of isotopic ratios were performed on a ThermoFinnigan Triton© mass spectrometer in static mode (University of Göttingen, Department of Isotope Geology). The mean ^{87}Sr/^{86}Sr ratio obtained for the Sr standard SRM NBS987 during the period of analytical work was 0.710272 ± 0,000039 (n = 8, 2σ). The Sr isotopic ratio was normalized to an ^{88}Sr/^{86}Sr ratio of 0.1194 over the course of this study. Total procedure blanks were consistently below 150 pg. The measured ^{87}Sr/^{86}Sr ratio was corrected for blank and mass fractionation, and after these corrections the ^{87}Sr/^{86}Sr ratio was adjusted to 0.710248 for the NBS987, which is the normalization ratio for the LOWESS curve and look-up table version 5.0 of McArthur et al. (44). The absolute age was translated into a geologic stage based on Gradstein et al. (45).

Oxygen isotopes. Samples for oxygen isotope analyses were extracted from the polished surfaces of the counterparts of the thin sections using a handheld microdrill. For O isotope analyses, carbonate powders were reacted with 100% phosphoric acid at 75°C using a Finnigan Kiel IV Carbonate Device attached to a Finnigan DELTA V PLUS mass spectrometer. All values are reported (per mil) relative to the Vienna Pee Dee belemnite standard (PDB) by assigning a $\delta^{18}O$ value of 2.20‰ to NBS19. Reproducibility was checked by replicate analysis of laboratory standards and was better than 0.05‰. To estimate paleotemperatures we used the formula of Epstein et al. (46) and assuming a seawater $\delta^{18}O$ value of –0.1‰ for the earliest Oligocene (32 Ma) (47); for the barnacle we subtracted 1.3‰ from the $\delta^{18}O_{carbonate}$ value to account for the vital effects among barnacles compared to calcitic mollusk shells (48). Results are summarized in Table 1.

SRXTM. Synchrotron Radiation X-ray Tomographic Microscopy (SRXTM) radiographs were collected at Beamline 8.3.2 of the Advanced Light Source at Lawrence Berkeley National Laboratory in Berkeley, California. This beamline is based on a 4.37 Tesla superbend magnet with critical energy of 11.5 keV. To penetrate the thick sample, "white light mode" was used (the monochromator mirrors are removed from the beam path) with a 3mm copper filter inserted to block softer X-rays. Detection was accomplished with a 0.5 mm LuAG:Ce scintillator and a 1x objective with a PCO.4000 CCD camera with pixel dimension of 4008x2672; a limited vertical portion of the detector was used, matching the beam height. A series of 7 tiles were collected to cover the full sample. For each tile, 2049 images were collected over 180 degrees, with exposure time of 450 ms. Preprocessing to remove zingers from the radiographs and to darkfield correct and normalize them by bright fields was performed by a custom ImageJ plugin, and tomographic reconstruction was performed with Octopus. The resulting voxel size was 7.4x7.4x7.4 um3. Tiles were digitally overlapped, and the pixels along the seams were intensity corrected to match the adjacent pixels. Because the intensity of the structures of interest was similar to the structures of the surrounding sample, simply volume rendering the reconstructed volume does not yield a useful visualization of these structures. There are subtle density differences at the edges of the relevant structures. For a region of interest, the boundaries of the structures were traced by hand using the Avizo software package. The boundaries were then used as a mask for the original data, which was then volume rendered using appropriate colormaps.

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References

1. R. S. Steneck *et al.*, Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* **29**, 436-459 (2002).
2. H. Teagle, S. J. Hawkins, P. J. Moore, D. A. Smale, The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology* **492**, 81-98 (2017).
3. J. J. Bolton, The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. *Helgoland Mar. Res.* **64**, 263-279 (2010).
4. K. A. Krumhansl *et al.*, Global patterns of kelp forest change over the past half-century. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 13785-13790 (2016).
5. S. Bennett *et al.*, The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. *Mar. Freshwater Res.* **67**, 47-56 (2016).
6. L. E. Graham, J. E. Graham, L. W. Wilcox, *Algae. 2nd ed.* (Benjamin Cummings, San Francisco, 2009), pp. 616.
7. J. S. Pearse, L. F. Lowry, *An annotated species list of the benthic algae and invertebrates in the kelp forest community at Point Cabrillo, Pacific Grove, California* (Coastal Marine Laboratory, University of California, Santa Cruz, Technical Report Number 1, ed. pdf, 1974), pp. 73.
8. H. L. Andrews, The kelp beds of the Monterey region. *Ecology* **26**, 24-37 (1945).
9. J. H. McLean, Sublittoral ecology of kelp beds of the open coast area near Carmel, California. *Biol. Bull.* **122**, 95-114 (1962).
10. D. R. Schiel, M. S. Foster, *The Biology and Ecology of Giant Kelp Forests* (University of California Press, Oakland, 2015), pp. 416.
11. J. Barron, "An updated diatom biostratigraphy for the Monterey Formation of California" in Siliceous microfossils and microplankton studies of the Monterey Formation and its modern analogues, R. Casey, J. Barron, Eds. (Society of Economic Paleontologists and Mineralogists, Pacific Section, Los Angeles, 1986), vol. 45, pp. 105–119.
12. B. C. Parker, E. Y. Dawson, Non-calcareous marine algae from California Miocene deposits. *Nova Hedwigia* **10**, 273-295 (1965).
13. J. A. Estes, P. D. Steinberg, Predation, herbivory, and kelp evolution. *Paleobiol.* **14**, 19-36 (1988).
14. J. Velez-Juarbe, D. P. Domning, N. D. Pyenson, Iterative evolution of sympatric seacow (Dugongidae, Sirenia) assemblages during the past ~26 million years. *PLoS ONE* **7**, e31294 (2012).
15. G. W. Saunders, L. D. Druehl, Nucleotide sequences of the small-subunit ribosomal RNA genes from selected Laminariales (Phaeophyta): implications for kelp evolution. *J. Phycol.* **28**, 544–549 (1992).

16. T. Silberfeld *et al.*, A multi-locus time-calibrated phylogeny of the brown algae (Heterokonta, Ochrophyta, Phaeophyceae): Investigating the evolutionary nature of the "brown algal crown radiation". *Mol. Biol. Evo.* **56**, 659-674 (2010).

17. S. Starko *et al.*, A comprehensive kelp phylogeny sheds light on the evolution of an ecosystem. *Mol. Phylo. Evo.* **136**, 138-150 (2019).

18. D. P. Domning, Kelp evolution: a comment. *Paleobiol.* **15**, 53-56 (1989).

19. P. D. J. Snavely, A. R. Niem, N. S. MacLeod, J. E. Pearl, W. W. Rau, Makah Formation - A deep-marginal-basin sequence of late Eocene and Oligocene age in the northwestern Olympic Peninsula, Washington. *U.S. Geol. Surv. Prof. Pap.* **1162**, 1-28 (1980).

20. A. I. Smith, The comparative histology of some of the Laminariales. *American Journal of Botany* **26**, 571–585 (1939).

21. T. T. Bringloe *et al.*, Phylogeny and evolution of the brown algae. *Critical Reviews in Plant Sciences* **39**, 281-321 (2020).

22. M. Velásquez, C. I. Fraser, W. A. Nelson, F. Tala, E. C. Macaya, Concise review of the genus *Durvillaea* Bory de Saint-Vincent, 1825. *Journal of Applied Phycology* **32**, 3–21 (2020).

23. H. Kawai, T. Hanyuda, L. M. Ridgway, K. Holser, Ancestral reproductive structure in basal kelp *Aureophycus aleuticus*. *Scientific Reports* **3**, 2491 (2013).

24. H. Kawai, T. Hanyuda, S. Uwai, "Evolution and biogeography of laminarialean kelps" in Seaweed Phylogeography, Z.-M. Hu, C. Fraser, Eds. (Springer, 2016), pp. 227-249.

25. S. D. A. Smith, R. D. Simpson, S. C. Cairns, The macrofaunal community of *Ecklonia radiata* holdfasts: Description of the faunal assemblage and variation associated with differences in holdfast volume. *Australian Journal of Ecology* **21**, 81-95 (1996).

26. H. Teagle, P. J. Moore, H. Jenkins, D. A. Smale, Spatial variability in the diversity and structure of faunal assemblages associated with kelp holdfasts (Laminaria hyperborea) in the northeast Atlantic. *PLOS ONE* **13**, e0200411 (2018).

27. P. K. Dayton, Ecology of kelp communities. *Annual Review of Ecology and Systematics* **16**, 215-245 (1985).

28. G. J. Vermeij *et al.*, The coastal North Pacific: Origins and history of a dominant marine biota. *J. Biogeogr.* **46**, 1-14 (2018).

29. G. J. Vermeij, Comparative biogeography: innovations and the rise to dominance of the North Pacific biota. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20182027 (2018).

30. K. H. Mann, Seaweeds: their productivity and strategy for growth. *Science* **182**, 975–981 (1973).

31. D. P. Domning, Sirenian evolution in the North Pacific Ocean *University of California Publications in Geological Sciences* **118**, 1-176 (1978).

32. L. G. Barnes, J. L. Goedert, Stratigraphy and paleoecology of Oligocene and Miocene desmostylian occurrences in western Washington State, USA. *Bulletin of the Ashoro Museum of Paleontology* **2**, 7-22 (2001).

33. S. Hayashi *et al.*, Bone inner structure suggests increasing aquatic adaptations in Desmostylia (Mammalia, Afrotheria). *PLoS ONE* **8**, e59146 (2013).

34. G. Mayr, J. L. Goedert, New late Eocene and Oligocene plotopterid fossils from Washington State (USA), with a revision of "*Tonsala*" *buchanani* (Aves, Plotopteridae). *J. Paleont.* **96**, 224-236 (2021).

35. J. F. Parham, J. A. Barron, J. Velez-Juarbe, "Middle and late Miocene marine mammal assemblages from the Monterey Formation of Orange County, California" in Understanding the Monterey Formation and Similar Biosiliceous Units across Space and Time, I. W. Aiello, J. A. Barron, A. C. Ravelo, Eds. (Geological Society of America, 2022), vol. 556, pp. 13 p.

36. Z. J. Tseng, C. Grohé, J. J. Flynn, A unique feeding strategy of the extinct marine mammal *Kolponomos*: convergence on sabretooths and sea otters. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20160044 (2016).

37. D. P. Domning, An ecological model for late Tertiary sirenian evolution in the North Pacific Ocean. *Syst. Zool.* **25**, 352-362 (1976).

38. W. O. Addicott, Tertiary climatic change in the marginal Northeastern Pacific Ocean. *Science* **165**, 583-586 (1969).

39. M. Steinthorsdottir *et al.*, The Miocene: the future of the past. *Paleoceanogr. Paleoclimat.* 10.1029/2020PA004037, e2020PA004037 (2021).

40. J. A. Estes, D. R. Lindberg, C. Wray, Evolution of large body size in abalones (*Haliotis*): patterns and implications. *Paleobiol.* **31**, 591-606 (2005).

41. A. B. Smith, Phylogenetic relationship, divergence times, and rates of molecular evolution for camarodont sea urchins. *Mol. Biol. Evo.* **5**, 345-365 (1988).

42. R. W. Boessenecker, A Middle Pleistocene sea otter from northern California and the antiquity of *Enhydra* in the Pacific Basin. *Journal of Mammalian Evolution* **25**, 27-35 (2018).

43. J. C. Zachos, M. Pagani, L. Sloan, E. Thomas, K. Billups, Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**, 686-693 (2001).

44. J. M. McArthur, R. J. Howarth, G. A. Shields, "Strontium isotope stratigraphy" in The Geologic Time Scale 2012, F. M. Gradstein, J. G. Ogg, M. Schmitz, G. Ogg, Eds. (Elsevier, 2012), pp. 127-144.

45. F. M. Gradstein, J. G. Ogg, M. Schmitz, G. Ogg, Eds., *The Geologic Time Scale 2012* (Elsevier, 2012), p 1176.

46. S. Epstein, R. Buchsbaum, H. A. Lowenstam, H. C. Urey, Revised carbonate-water isotopic temperature scale. *Geol. Soc. Am. Bull.* **64**, 1315-1326 (1953).

47. C. H. Lear, H. Elderfield, P. A. Wilson, Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite. *Science* **287**, 269-272 (2000).

48. J. S. Killingley, W. A. Newman, ^{18}O fractionation in barnacle calcite: a barnacle paleotemperature equation. *J. Mar. Res.* **40**, 893-902 (1982).

The authors declare no competing interest.

Figure captions

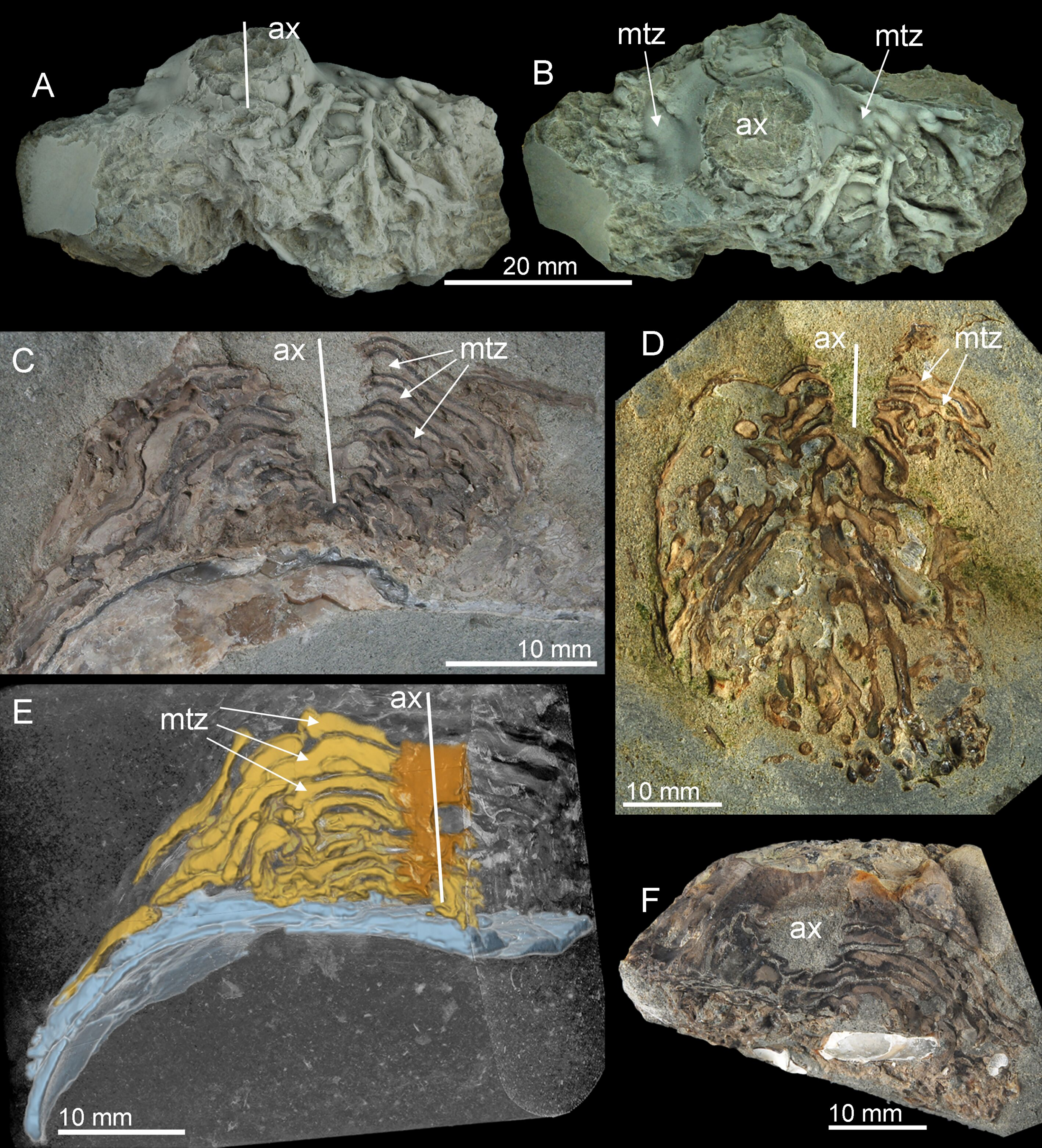
Fig. 1. Earliest Oligocene kelp holdfasts from the Jansen Creek Member of the Makah Formation in western Washington State, USA. From the central axis (ax, marked by white lines) extends a lobe-like meristematic transition zone (mtz) that divides into branching, finger-like haptera; the axis represents the conical base of the stipe and is not preserved in any of the specimens. (A, B) NRM S169277. (C) UCMP 201250. (D) NRM S126523. (E) SRXTM 3D reconstruction of same specimen as in fig. C; blue = bivalve shell, yellow = haptera, ochre = inferred conical base of stipe. (F) NRM S126528.

Fig. 2. Earliest Oligocene kelp holdfasts from the Jansen Creek Member of the Makah Formation in western Washington State, USA. (A) Cross section through mass of haptera, barnacle plate in upper left (NRM S126522). (B) Cellular detail of finger-like hapteron; tcw = thickened cell wall (UCMP 201251.01). (C) Haptera attached to barnacle surface (UCMP 201251.01). (D) Haptera overgrowing a barnacle; note sediment-filled but haptera-free interior of barnacle (NRM S126521). (E) Small bivalve shell overgrown by haptera (NRM S126521). (F) Holdfast growing on two upright mussel shells (white arrows; same specimen as on Fig. 1F; NRM S126528). (G) Mass of haptera encasing axially ribbed gastropod shell (NRM S126522). (H) Haptera growing on gastropod shell (left arrow) and a piece of clastic sediment (right arrow) (NRM S126522).

Fig 3. Stratigraphic occurrence of fossil kelps and associated organisms; green bars indicate members of early kelp beds, black bars indicate members of the modern, complex kelp ecosystems. Temperature curve are planktonic foraminiferans oxygen isotope data (43); *Julescraneia* specimen has UCMP specimen number 250230 and also LACM PB-1524; see text for sources of stratigraphic ranges.

Table 1. Carbon and oxygen isotope data.

Sample	**δ^{13}C (PDB) [‰]**	**δ^{18}O (SMOW) [‰]**	**Paleotemperature (°C)**
Barnacle shell (calcite) with holdfast (UCMP 201251)			
	2.287	32.232	15.6
	2.047	32.061	16.4
	0.89	32.148	16.0
	2.006	31.955	16.8
Pteriomorph bivalve shell (calcite) with holdfast (UCMP 201250)			
	1.415	30.241	19.9
	0.145	30.062	21.0
	0.076	29.757	23.0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ax
B
mtz
mtz
ax
20 mm
C
ax
mtz
10 mm
D
ax
mtz
10 mm
E
mtz
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F
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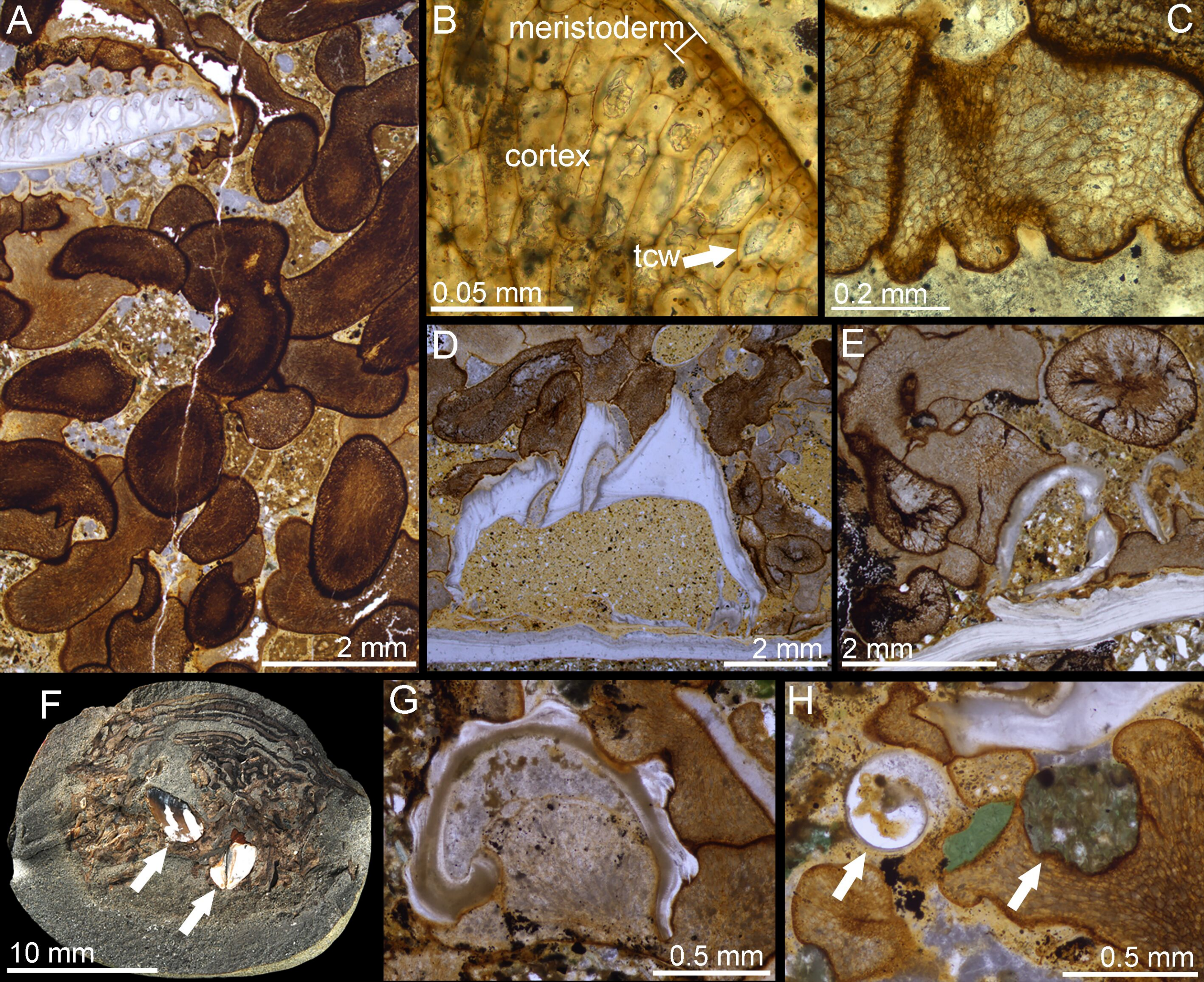
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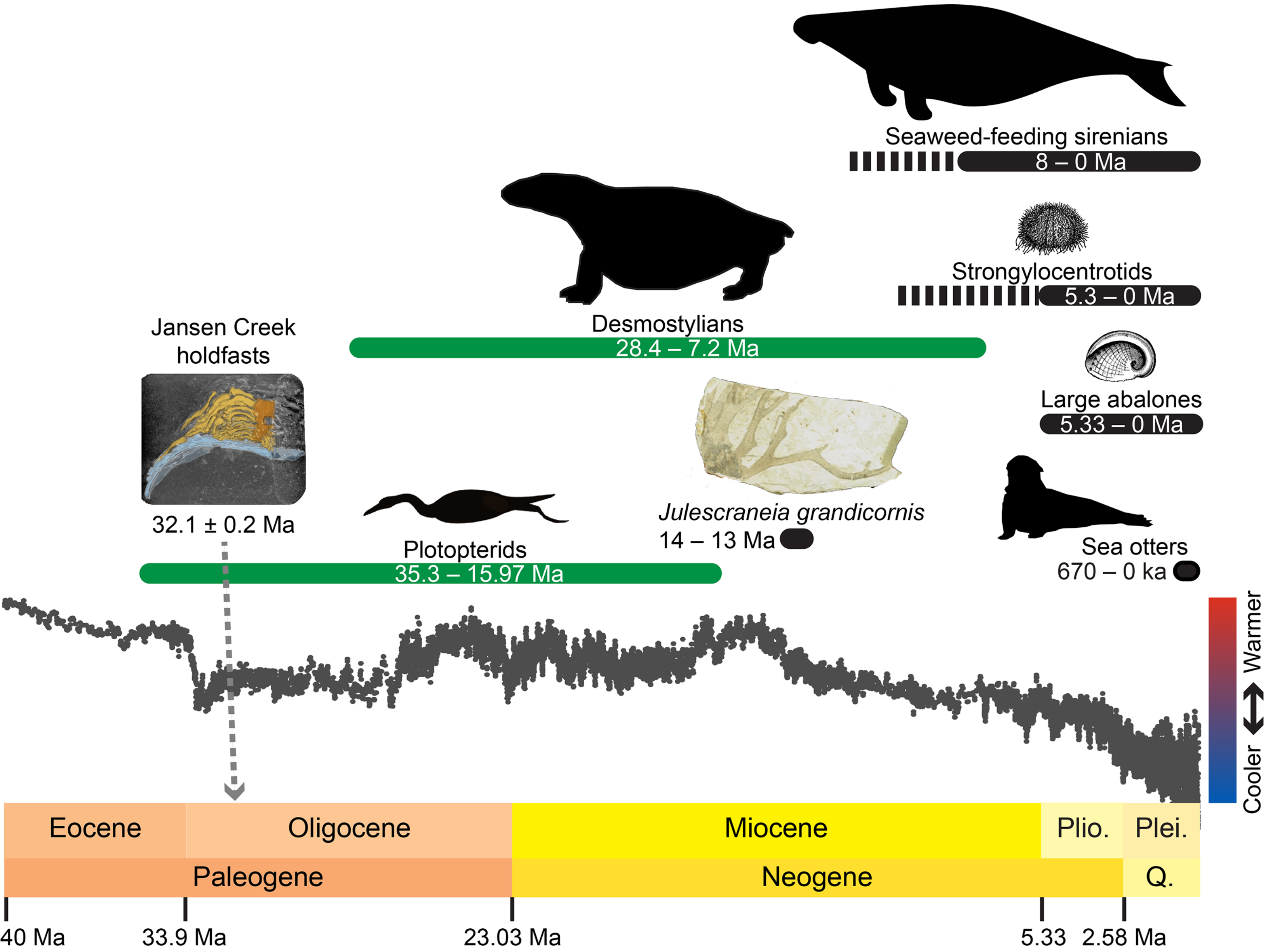
B
meristoderm
cortex
tcw
0.05 mm
C
0.2 mm
D
2 mm
E
2 mm
F
10 mm
G
0.5 mm
H
0.5 mm


Seaweed-feeding sirenians
8 – 0 Ma
Strongylocentrotids
5.3 – 0 Ma
Large abalones
5.33 – 0 Ma
Sea otters
670 – 0 ka
Desmostylians
28.4 – 7.2 Ma
Jansen Creek
holdfasts
32.1 ± 0.2 Ma
Julescraneia grandicornis
14 – 13 Ma
Plotopterids
35.3 – 15.97 Ma
Warmer
Cooler
Eocene
Oligocene
Miocene
Plio.
Plei.
Paleogene
Neogene
Q.
40 Ma
33.9 Ma
23.03 Ma
5.33
2.58 Ma