A modern scleractinian coral with a two-component calcite–aragonite skeleton

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Edited by Paul G. Falkowski, Rutgers University, New Brunswick, NJ, and approved November 4, 2020 (received for review June 29, 2020)

One of the most conserved traits in the evolution of biomineralizing organisms is the taxon-specific selection of skeletal minerals. All modern scleractinian corals are thought to produce skeletons exclusively of the calcium-carbonate polymorph aragonite. Despite strong fluctuations in ocean chemistry (notably the Mg/Ca ratio), this feature is believed to be conserved throughout the coral fossil record, spanning more than 240 million years. Only one example, the Cretaceous scleractinian coral Coelosmilia (ca. 70 to 65 Ma), is thought to have produced a calcitic skeleton. Here, we report that the modern asymbiotic scleractinian coral Paraconotrochus antarcticus living in the Southern Ocean forms a two-component carbonate skeleton, with an inner structure made of high-Mg calcite and an outer structure composed of aragonite. P. antarcticus and Cretaceous Coelosmilia skeletons share a unique microstructure indicating a close phylogenetic relationship, consistent with the early divergence of P. antarcticus within the Vacatina (i.e., Robusta) clade, estimated to have occurred in the Mesozoic (ca. 116 Mya). Scleractinian corals thus join the group of marine organisms capable of forming bimineralic structures, which requires a highly controlled biomineralization mechanism; this capability dates back at least 100 My. Due to its relatively prolonged isolation, the Southern Ocean stands out as a repository for extant marine organisms with ancient traits.

Significance

Until now, all of the ca. 1,800 known modern scleractinian coral species were thought to produce skeletons exclusively of aragonite. Asymptotic Paraconotrochus antarcticus living in the Southern Ocean is the first example of an extant scleractinian that forms a two-component carbonate skeleton, with an inner structure made of high-Mg calcite and an outer structure composed of aragonite. This discovery adds support to the notion that the coral skeletal formation process is strongly biologically controlled. Mitophylogenic analysis shows that P. antarcticus represents an ancient scleractinian clade, suggesting that skeletal mineralogy/polymorph of a taxon, once established, is a trait conserved throughout the evolution of that clade.

The ability to form a calcium carbonate skeleton represents an evolutionary innovation of major importance that dates back to the onset of the Phanerozoic (ca. 540 Ma) (1). Since that time, multiple groups of marine metazoans became highly efficient reef builders, creating the structural foundation for the richest and most biodiverse ecosystems in the ocean (2). In our modern ocean, carbonate reef building is dominated by scleractinian corals, which produce ~1012 kg of skeleton carbonate every year (3). Based on available empirical evidence, it is widely accepted that pristine skeletons of modern scleractinians, grown in natural environments, consist exclusively of the carbonate polymorph aragonite, which is metastable at ambient conditions typical of the Earth’s surface.

In vitro experiments under ambient temperatures show that abiogenic precipitation of calcium carbonate polymorphs from seawater is controlled primarily by the Mg/Ca ratio (4). With present-day ionic strengths and atmospheric CO2 concentration (pH ca. 8), the seawater Mg/Ca ratio (today 5.2 mol/mol) separates two regimes of inorganic carbonate polymorph precipitation: the regime of low-magnesium calcite (LMC) at Mg/Ca < 2 mol/mol (“calcitic seas”) and the regime of aragonite and/or high-Mg calcite (HMC) precipitation at Mg/Ca > 2 mol/mol (“aragonitic seas”) (5, 6). During the mid-Cretaceous, the Mg/Ca ratio is thought to have been well below 2 mol/mol (7, 8), creating conditions conducive to calcite precipitation. Despite that, only one scleractinian coral, Coelosmilia from Upper Cretaceous chalk deposits, has, to date, been documented to have a bona fide primary calcitic skeleton (9). This observation is consistent with biomineralizing organisms exerting stronger control over polymorph selection than a simple inorganic precipitation process.

Coral skeletal microstructural patterns are highly conserved through evolution and have often been used to elucidate phylogenetic relationships in the absence of genetic information (10). Corals exhibiting similar microstructure very likely share a similar origin. Indeed, the biomineralization process has proven to be robust enough to withstand dramatic environmental changes throughout geological time, including substantial changes in seawater chemistry (11, 12).

In this context, we report the discovery that the extant, deep-sea, solitary, scleractinian coral Paraconotrochus antarcticus, which is ubiquitous in the Southern Ocean around Antarctica...
(13) at depths between 50 and 700 m and at temperatures between ca. 0.5 and 3 °C, forms a two-component calcite–aragonite skeleton with microstructural features very similar to the Cretaceous Coelosmilia (Fig. 1 and SI Appendix, Fig. S1).

Results

The samples of P. antarcticus studied here include both bare skeletons and specimens collected alive, obtained from material dredged from the Weddell, Ross, and Cooperation seas, respectively (SI Appendix, Fig. S2 and Table S1). The skeleton of P. antarcticus is shaped like a regular cone, which is a few centimeters in both diameter and height (Fig. 1 A and B and SI Appendix, Fig. S1 A and B). Its septa are hexamernally arranged in five cycles, and the central portion of the calcite is occupied by labyrinthine projections (so-called columnella).

In transversal cuts (n = 31), all examined P. antarcticus consistently revealed a distinct boundary between two main skeletal regions, hereafter referred to as the inner and outer skeleton (Fig. 1 E, F, and H–J). The inner skeleton is relatively narrow (ca. 50 to 100 µm thick) and forms the central parts of the septa and wall (Fig. 1 E and H–J). This inner skeleton is also observable at the distalmost (upper) growth front of the calice, where it is deposited quasi-contemporaneously with the outer skeleton (Fig. 1 C and D). Microstructurally, the inner skeleton consists of rapidly accreted deposit (RADs; ca. 10 µm in diameter, also referred to as “centers of calcification”) that define the central axis, and “fibrous” skeleton, or thickening deposits (TDs) ca. 20 to 30 µm thick, which consist of relatively broad ca. 10 µm bundles of fibers, completely transparent in transmitted light and flanking the RAD region (Fig. 2 A and B).

A sharp crystallographic boundary delineates the transition from the inner skeleton to the outer skeleton (Fig. 2 F–H). In those regions where the outer skeleton is in direct contact with the inner skeleton, the former typically consists of long (often >100 µm) and relatively narrow (ca. 5 µm) bundles of crystal fibers (Fig. 2G). However, as the outer skeleton continues to form beyond the inner skeleton, it consists of the same two classical microstructural components (i.e., RADs overgrown by fibrous TDs, such as in Fig. 2 J and SI Appendix, Figs. S3B, S5C, and S7 E and F). In contrast to the majority of other modern scleractinians, but in close structural analogy with Cretaceous Coelosmilia, the outer skeleton is gradually covered with a third carbonate structure that progressively infills the entire lumen of the calice bottom-up (SI Appendix, Figs. S1, S3–S6, and S9 A and B).

All of these skeletal regions and components exhibit the nanoparticulate texture characteristic of biogenic minerals (14) when observed by scanning electron microscopy (SEM) and atomic force microscopy (AFM) (Fig. 2 C–E).

However, the observation of different calcium-carbonate polymorph compositions between the inner (calcite) and outer (aragonite) skeletons sets P. antarcticus apart from all other living scleractinian corals. The calcitic mineralogy of the inner skeleton is unequivocally demonstrated by both electron backscatter diffraction and Raman spectroscopy imaging of thin sections (Figs. 1G and J and SI Appendix, Fig. S10). The density difference between calcite and aragonite (2.65 to 2.71 g/cm³ versus 2.94 g/cm³) makes these polymorphs distinguishable with high-resolution three-dimensional (3D) tomography, which revealed that the calcitic inner skeleton is a corrugated (and occasionally perforated/discontinuous) structure forming the central plane of the septa and wall (Fig. 1 E and F). Both 3D tomography and serial thin sectioning showed that the inner calcitic skeleton is usually present throughout the skeletal ontogeny (SI Appendix, Figs. S3–S6), although some specimens exhibited discontinuities in the development of the inner skeletal structure, typically accompanied by concentrically grown deposits (SI Appendix, Figs. S7 and S8). As expected, there is a sharp difference in chemical composition between the calcitic and aragonitic regions (Fig. 2 L and M). The calcitic inner skeleton is depleted in Sr and Na and enriched in Mg, averaging ca. 11 mole percent (mol%) of MgCO₃ and thus compositionally HMC, which is consistent with the observed Raman peak shifts relative to the LMC (Fig. 2F). The aragonitic outer skeleton contains ca. 1.2 mol% SrCO₃, with MgCO₃ below the electron microprobe detection limit, that is, similar to aragonitic skeletons of other deep-sea corals (15).

Both aragonitic and calcitic crystals have the a and b axis rotated around the c axis (turbostatic distribution) in the plane (222) of aragonite and (1014) of calcite (Fig. 2 F–H). Raman spectra in RADs and neighboring TD regions indicated disordered material in both calcite and aragonite RADs (Fig. 2 I–K). The aragonitic RADs showed stronger fluorescence than RADs in the calcitic inner skeleton (SI Appendix, Fig. S9 A and B).

The measured average ⁴⁴Ca/⁴⁰Ca isotope ratios of the aragonitic and calcitic skeletal parts were −1.51 ± 0.21‰ and −1.24 ± 0.14‰ (relative to seawater, 2R). The mean δ⁴⁴/⁴⁰Ca value of the inner calcitic skeleton is consistent with that observed in other biomineralizers that form HMC and have sophisticated control over biomineralization. The average δ⁴⁴/⁴⁰Ca value of the aragonitic outer skeleton is consistent with other biogenic aragonites. The difference in the average oxygen isotopic composition between the calcitic inner and the aragonitic outer skeletons is less than 1‰ (SI Appendix, Fig. S15).

All these unique skeletal features of the P. antarcticus point to a distinct position of this taxon in the phylogeny of Scleractinia. To investigate this, we performed a mitophylogenomic analysis that involved all mitochondrial protein-encoding genes of P. antarcticus aligned to those from 57 other scleractinarians and 12 corallimorpharians, the latter used as an outgroup (SI Appendix, Table S2). The resulting phylogeny placed P. antarcticus in an early diverging position within the Vacuum- (Robusta) clade, with time calibration indicating a Cretaceous (ca. 116 Ma) divergence of its lineage (Fig. 5).

Discussion

Although calcite deposits can be observed in adult skeletons of modern scleractinarians, these are invariably considered to be secondary calcite cements or products of calcite precipitation induced by other organisms, such as skeletal borers and/or microbes (16, 17). The occurrence of HMC in P. antarcticus skeleton was noted previously (18) but interpreted as diagenetic infilling of microborer cavities. It is, however, highly unlikely that the calcitic inner skeleton of P. antarcticus is the result of alteration by other organisms, such as skeletal borers and/or microbes (16, 17). The occurrence of HMC in P. antarcticus skeleton was noted previously (18) but interpreted as diagenetic infilling of microborer cavities. It is, however, highly unlikely that the calcitic inner skeleton of P. antarcticus is the result of alteration by other organisms, such as skeletal borers and/or microbes (16, 17).
with a continuous assemblage of amorphous intermediate precursors (i.e., amorphous calcium carbonate [ACC]) (14, 20–23). If a diagenetic process had transformed ACC into calcite and aragonite postmortem, that is, in the absence of a continued biomineralization process, the difference in molar volume between the ACC (ca. 54 cm³/mol) and calcite or aragonite (both

**Fig. 1.** Extant specimen of the solitary scleractinian coral *Paraconotrochus antarcticus* with a two-component calcitic (inner)–aragonitic (outer) skeleton. Distal (A) and lateral (B) views of the calice are shown. (C and D) The growth edges of the septa and wall exhibit a calcitic inner skeleton (white arrows) overgrown by an aragonitic outer skeleton (yellow arrows); blue- and red-crossed circles mark the position of micro-Raman analyses. (E) A Raman map (region marked in E) showing the distribution of calcite (blue) and aragonite (beige) in a skeleton sectioned transversely. (F) Raman spectra (from 0 to 1,500 cm⁻¹) that include both lattice and internal [v1, v4], vibrational modes) of coral aragonite (beige) and calcite (blue) collected from regions indicated in C. (H–J) Transverse sections of adult (H), juvenile (I), and early juvenile (J) parts of the calice. Distinct boundaries (i.e., heteroepitaxy) between the crystal-transparent calcitic regions (with dark RADs) and the brownish aragonitic regions are visible. (K and L) X-ray computed tomography visualization of the calcitic inner (blue) and the aragonitic outer skeleton (semitransparent beige) up to the level indicated with a dashed line in B. (A–C, E, and G) ZPAL H.25/114; (D) ZPAL H.25/115; (E and F) ZPAL H.25/116; (H, I, and J) ZPAL H.25/117.
Fig. 2. The microstructural, crystallographic, and geochemical features of calcitic and aragonitic regions of Paraconotrochus antarcticus skeleton. (A and B) The calcitic inner skeleton consists of RADs (arrows) and fibrous layers (i.e., TDs). (C–E) SEM of a transversely sectioned skeleton with a dashed frame indicating the region enlarged in A, whereas blue (D) and black (E) circles mark areas observed by AFM. Both calcitic (D) and aragonitic (E) skeletal parts have a nanogranular texture, typical of biominerals. (F–H) The sharp crystallographic boundary between the inner calcitic and outer aragonitic skeleton (G); in both regions, crystals have their a and b axes rotating around a c axis (turbostratic distribution: calcite (F) in the plane 1014 and aragonite (H) in the plane 222. (I–K) The Raman spectra in RADs and neighboring TD regions (numbers in J mark measurement points) indicate disordered material in both calcite (I) and aragonite RADs (K), consistent with biogenic formation from amorphous precursors. (J) A Raman map. (L–O) Back-scattered electron (BSE) and electron microprobe images show the expected contrasting trace-element distributions, with calcite enriched in Mg (M) and depleted in Sr (N) and Na (O) compared with aragonite. (A–E and L–O) ZPAL H.25/117; (F–K) ZPAL H.25/116.
ca. 37 cm$^2$/mol) would result in clearly visible porosity, which was not observed. 5) A primary origin of the P. antarcticus skeleton is also supported by the crystallographic arrangement of aragonitic and calcitic crystals that have a and b axes rotated around the c axis (turbosstratic distribution), which is considered to be a biogenic strategy to prevent crystal cleavage (Fig. 2) (24, 6) The distalmost edge of the septa, which represents the growth-edge, and hence the most recently formed skeleton, exhibits the same calcitic component as septal regions deeper in the calice (inner skeleton). If the inner skeleton is the result of a transformation from aragonite, or another precursor (for example, ACC), this transformation must be nearly instantaneous.

A primary biogenic origin of the inner calcitic skeleton is also supported by its stable isotopic compositions. The measured average $^{44}$Ca/$^{40}$Ca isotope ratios of the aragonitic and calcitic skeletal parts are consistent with the values observed for biocalcifiers with skeletons of similar mineralogy and recognized to exert strong control over their biomineralization process (25, 26) (SI Appendix, Figs. S13 and S14 and Table S3). In addition, low Sr/Ca and high Mg/Ca ratios indicate that the calcite $^{44}$Ca/$^{40}$Ca did not result from closed-system diagenetic recrystallization of aragonite to calcite (27, 28). Open-system diagenetic recrystallization would have shifted calcium isotope ratios to much higher values ($^{44}$Ca/$^{40}$Ca > -1‰) (SI Appendix, Fig. S13). The average oxygen isotope composition between the calcitic inner and the aragonitic outer skeletons is less than 1‰, which is consistent with observations of, for example, bimineralic bivalves (29). Furthermore, the oxygen isotopic variability observed at the micrometer scale in the inner- and outer-skeletal parts is similar to that observed in other coral skeletons (30, 31) and can only be ascribed to vital effects (SI Appendix, Figs. S15 and S16 and Table S4) (15, 30). We thus conclude that the inner calcitic skeleton in P. antarcticus is pristine and the result of a highly controlled biomineralization mechanism as opposed to secondary alteration.

The evolutionary stability of skeletal mineralogy and biomineralization patterns of scleractinian corals is now widely recognized (32). With regard to Paraconotrochus and Coelosmilia, this implies that they may very well have had a common evolutionary history. The mitophylogenic analysis indicated a Cretaceous (ca. 116 Ma) divergence of its lineage (Fig. 3), coinciding with the lowest ocean Mg/Ca ratio during the Phaner-ozoe (<1 mol/mol). Culturing experiments have suggested that low-Mg seawater chemistry strongly affects the expression of genes related to coral skeletal formation and may trigger a change from aragonite to calcite mineralogy (33). Other experiments have demonstrated a physiologically controlled calcite-to-aragonite mineralogical switch triggered by changes in the growth solution Mg/Ca ratio (21, 34, 35). Although the majority of coral lineages that survived through the major changes in the oceanic Mg/Ca ratio continued to produce aragonitic skeletons, Cretaceous Coelosmilia was capable of developing a purely calcitic corallum (9). P. antarcticus, which has skeletal morphology and microstructure very similar to Coelosmilia (SI Appendix, Fig. S1), may be a direct descendant of this (or another) Mesozoic coral lineage capable of depositing a calcitic skeleton.

**Conclusions and Perspective**

This discovery of a two-component calcite–aragonite skeleton produced by extant P. antarcticus offers an opportunity to greatly enhance the understanding of the scleractinian biomineralization process, which, necessarily, is highly controlled by the animal. It also provides a unique window into the evolutionary history of scleractinian corals and changes the basis for theories about scleractinian coral evolution through geological time (during which ocean chemistry varied substantially to favor either aragonite or calcite production) by removing the obstacle that skeletal mineralogy defines an impassable boundary between higher level anthozooan taxonomic units.

Despite dramatic physicochemical changes of the marine environment(s) surrounding the Antarctic continent since the Mesozoic (36), the Southern Ocean is recognized as an evolutionary refuge for numerous benthic invertebrates. Among these, about 30 modern Southern Ocean molluscan genera already existed in the late Cretaceous–early Paleogene (37). The long-term survival of these benthic metazoans in the Southern Ocean can be ascribed to its relative isolation and unique environmental conditions over the last 100 Myr (38). The presence of early-diverging P. antarcticus in the Southern Ocean suggests that this region has also played an important role as refuge for the evolution of asymbiotic scleractinian corals. The corals living there may carry the answer to a series of fundamental evolutionary questions: what are the genetic and/or environmental underpinnings of the calcite-forming capability in corals? Is the Paraconotrochus the only living scleractinian capable of calcite skeleton formation? Was there a higher diversity of such corals in the geological past? Is the mineralogical difference still to be considered a major obstacle for evolutionary transition between Paleozoic rugosan and scleractinian corals (39)?

Today, anthropogenic climate change and ocean acidification are rapidly impacting the polar regions. High-latitude seawater is predicted to become undersaturated with respect to aragonite and high-Mg calcite within a few decades because of ocean uptake of anthropogenic CO$_2$. Such changes represent an existential threat to marine calcifying organisms (40, 41) endemic to these regions. The observations presented here further emphasize the uniqueness of the Southern Ocean as a repository for ancient traits and an important window into the evolutionary history of marine benthic organisms. We have much more to learn from these environments and their inhabitants, which further enhances the need for their preservation.

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**Fig. 3.** The position of Paraconotrochus antarcticus (arrow) in phylogeny of the scleractinia. The early-diverging Gardineria hawaiiensis (“Basal”), the Vacatia (Robusta), and Refertia (Complexa) are shown. P. antarcticus has an early-diverging position within the Vacatina clade, from which it diverged in the Mesozoic (Cretaceous) ca. 116 Ma. The diagram is based on maximum likelihood (ML) and Bayesian inference of concatenated nucleotides from all mitochondrial protein-coding genes. Small red circles on nodes indicate ML and posterior probability support of 100 and 1, respectively. The numbers close to some nodes indicate estimated divergence times using a relaxed molecular clock (uncorrelated log-normal).
Materials and Methods

Materials. Detailed information about the material examined is provided in the SI Appendix, SI Materials. This study is based on the examination of a large collection of *P. antarcticus* from three major regions of the Southern Ocean (Weddell Sea, Ross Sea, and Cooperation Sea). In addition, specimens housed as dry skeletons, we also examined specimens of *P. antarcticus* collected alive in Weddell Sea and Cooperation Sea and preserved in 70% ethanol. Because of their excellent preservation condition, molecular analysis of specimens collected alive by the RRS James Clark Ross (British Antarctic Survey) off Antarctica in March 2016 was possible.

Methods: Skeletal Analyses

Atomic Force Microscopy. The AFM allows for the determination of the 3D surface topology of the biomineral at nanometer resolution. Following established procedures (42), measurements were performed using the Multi- mode 5 Atomic Force Microscopy instrument (Veeco) upgraded to Multimode 8 version (Bruker). The images have been acquired in ScanAsyst mode.

Cathodoluminescence microscopy. Cathodoluminescence is a method to determine the spatial distribution of primary and secondary features of carbonate samples. Diagenetic environments enriched with activator ions such as Mn are usually reducing (low Eh). Secondary calcite that was altered within a reducing diagenetic environment—in contrast to original carbonate skeleton—typically contains a high concentration of Mn⁸⁶ (the main activator of luminescence in carbonates) and exhibits strong orange to red luminescence. Cathodoluminescence of the thin-sectioned skeleton of *P. antarcticus* was examined with a hot cathode microscope HCM 6000 at the Laboratory of Applied Spectroscopy and Electron Confocal Microscopy at the Faculty of Biology (University of Warsaw) equipped with 488 nm lasers; a 32-channel spectral detector with a resolution of 2, 5, 6, or 10 nm; and mode Virtual Filter linked to Nikon’s DS-5Mc video camera with charged-coupled device detector with a resolution of 5 Mpx.

Electron microprobe analysis. The electron microprobe analysis mapping enables simultaneous analysis of different elements and the determination of distribution maps for each element with ca. 1 µm lateral resolution. The measurements were conducted on polished and C-coated thin sections with a JEOL Superprobe JZA-8900 equipped with five wavelength-dispersive spectrometers at the National Centre of Electron Microscopy (the Universidad Complutense of Madrid, Spain). Four elements (Ca, Mg, Sr, and Na) were mapped (800 × 800 points) (Fig. 2 K-M). An accelerating voltage of 20 kV with a beam current of 50 nA and a spot size and step interval of 1 nm in diameters were used.

Electron backscatter diffraction. The electron backscatter diffraction (EBSD) is a scanning electron microscope-based microstructural-crystallographic characterization technique that can provide information about, for example, the phase and crystal orientation in the material. Thin-sectioned samples were polished with alumina of 9 µm, 1 µm, and 0.3 µm and then with colloidal silica (0.05 µm). Before analysis, samples were cleaned, dried, and coated with a conducting carbon layer ca. 3 nm in thickness using a BALTEC SCD 005 sputter coater. The EBSD study was carried out with an Oxford NordlysMax detector mounted on a scanning electron microscope JEOL JSM-6610LV at the Institute of Materials Engineering, Lodz University of Technology. EBSD data were collected with AztecHKL software at high vacuum, 20 kV, large probe current, and 20 nm of working distance. EBSD patterns were collected at a resolution of 0.22 µm per pixel for crystallographic maps using the unit cell characteristics of aragonite and calcite as follows: *Pmcn* symmetry and a = 4.96 Å, b = 7.97 Å, and c = 5.75 Å estimated for *Favila* coral using X-ray powder diffraction with synchrotron radiation (43) and a = b = 4.99 Å, and c = 17.06 Å, respectively. EBSD data were processed using CHANNEL 5 software from Oxford Instruments. The EBSD data are represented as phase maps (showing the distribution of the different mineral phases), band contrast images (showing the quality of the material diffraction) corresponding to crystallographic orientation images with corresponding pole figures of aragonite and calcite in selected regions. The MATLAB toolbox MTEX (44) was used for the stereographic projection of crystallographic planes in reference to the (001), (010), (100), and (222) for aragonite and (0001), (0110), (1010), and (1014) for calcite.

Isotope analyses (calcium isotopes). Calcium isotope preparation and analyses were performed at Princeton University. The specimen was microdrilled using a Brasseler scriber point carbide drill bit (H1621.11.008 HP) on an ESI Micromill. The smallest available drill diameter (~100 µm) was used to drill precisely in the inner calcite skeleton and minimize introduction of the outer skeleton aragonite. Microdrilled carbonate was dissolved directly in 0.2% nitric acid for chromatography. Calcium was isolated from matrix elements on an automated Dionex ICS-5000+ ion chromatography system coupled with a Dionex AS-AP fraction collector using previously published methods (26, 27, 46). Following ion separation, samples were treated with concentrated HNO₃ and then dried and redissolved in 2% HNO₃ for mass spectrometry.

Calcium isotope ratios were measured on a Thermo Scientific Neptune Plus multicollector inductively coupled plasma mass spectrometer (MC-ICP-MS). Sample solution concentrations were carefully matched to a standard solution concentration of 2 ppm Ca to minimize concentration-dependent isotope effects. The analyses were performed with an ESI Apex-IR sample introduction system using medium resolution mode to avoid isobaric *Sr*²⁺ and Ar*H*⁺ interferences. Measured δ⁴⁴/⁴³Ca values were converted (48) to δ¹⁸/¹⁶O values assuming a mass-dependent fractionation with a slope of 2.05 and assuming no excess radiogenic *Ca*. All Ca isotope values were plotted in 3-isotope space (δ⁴⁴/⁴³Ca vs. δ¹⁸/¹⁶O) to verify that the Ca isotope ratios fell along the expected mass-dependent line.

All data are reported in delta notation relative to modern seawater (SMOW) with δ¹⁸/¹⁶O set at 0.0‰ (Fig. 3). We report long-term external reproducibility using the measured value of δ¹⁸/¹⁶O relative to modern seawater, both of which were corrected for the full chemical procedure (column chromatography and mass spectrometry) with each batch of samples. Our measured δ⁴⁴/⁴³Ca value for SMR915b relative to modern seawater is −1.22 ± 0.14‰ (δ¹⁸/¹⁶O = 0.23‰). In a recent study, we analyzed oxygen isotope ratios. The spot size was 10 to 15 µm, and no raster was used. *¹⁸O* and *¹⁶O* were collected simultaneously on Faraday cups with a mass resolution of ca. 2200. The electron flood gun, with normal incidence, was used to compensate charges. Mass calibration was performed at the beginning of each session using the *CaSO₄* (40–46) and *NaCl* (42) standards. Because of high mass resolution, we used the calibration of rollion-Bard and Marin-Carbonne (50). The reproducibility of the calcite standard was 0.38‰ (2 SDs), and the reproducibility of the aragonite standard was 0.23‰ (2 SDs) over the session. No drift correction was applied. *δ¹⁸O* is referred to the standard mean ocean water (PDB). *δ¹⁸O* ratio of 0.2505 ± 0.0025 (δ¹⁸O = 0.0005) was used.

Optical microscopy. Polished sections were examined using a Nikon Eclipse 80i transmitted light microscope fitted with a DS-5Mc cooled camera head. Observations were conducted in transmitted and polarized light. The morphological details of calcite–aragonite contact at distal parts of the septa and walls were examined by the Keyence VHX-5000 Digital Microscope at the Institute of Paleobiology, Warsaw, Poland (the help of Łucja Fostowicz-Frelik is greatly appreciated).

Cathodoluminescence. The Raman measurements were performed with LabRAM 800 HR confocal microscope (Horiba Jobin Yvon) equipped with a diode-pumped Nd:YAG laser (Spectra-Physics) operating at 532.3 nm (ca. 2 mW power on the sample). The individual spectra were recorded using 1,800 grooves/mm holographic grating, while for the acquisition of maps, the
600-groove/mm grating was used. The most convenient signals allowing for identification of the calcite and aragonite polymorphs are gained in the 100 cm–1 region. Calcium carbonate polymorphs associated with lattice vibrations, appear at 205 cm–1 and 153 cm–1 for aragonite and at 281 cm–1 and 153 cm–1 for calcite. The analysis of the maps was performed employing the modeling option of the Labspec software (Horiba Jobin Yvon).

**SEM.** Polished sections were lightly etched in Mutvei’s solution following described procedures (51) and then rinsed with Milli-Q water and air-dried. After drying, the specimens were put on stubs with double-sticking tape and sputter-coated with conductive platinum film. Analyses were made using a Phillips XL20 scanning electron microscope at the Institute of Paleobiology, Warsaw, Poland.

**X-ray microtomography.** The density difference between inner calcitic and outer aragonitic skeleton [in theory, 2.71 g/cm3 versus 2.93 g/cm3], but slightly lower in biominerals that contain organic inclusions (S2)] makes these skeletal regions distinguishable with high-resolution 3D tomography. Microcomputed tomography data were collected with Zeiss XRadia MicroCT-400 system at the Faculty of Materials Science and Engineering, Warsaw University of Technology Scans. Of a lower portion of ZPWL H.25/114 specimen of *P. antarcticus* were performed using the following parameters: voltage: 80 kV, power: 10 W, exposure time: 3 s, pixel size: 19.26 μm, 1,000 projections. Radial projections were reconstructed with XMReconstructor software. The 3D images of calcitic inner and aragonitic outer skeleton were obtained by processing with the AVIZO7.1 Fire Edition software.

**Methods: Molecular and Phylogenetic Analyses.** *P. antarcticus* total genomic DNA was extracted following a modified cetyltrimethylammonium bromide (CTAB) protocol (53) with an additional cleanup step using the Qiagen PowerClean Kit. DNA quality and yield were assessed and measured on a 1% agarose gel and Qubit 2.0 fluorometer, respectively. Library preparation, target enrichment of ultraconserved elements and exons, and sequencing details followed those provided in Quattrini et al. (54). Resulting sequences were assembled using Spades 3.10 (55), and the resulting nucleotide sequences from all mitochondrial protein coding genes. Mitophylogenomic Maximum Likelihood (ML) analyses were based on approximate likelihood ratio test using PhyML 3.0 (59) and 100 bootstrap replicates using RAxML (60) implemented at CIPRES (61) under the General Time Reversible (GTR) + G + I model of nucleotide substitution. Bayesian inference was performed on MrBayes also implemented at CIPRES with two runs each containing 100,000 generations saved at every 1,000, with a burn-in factor of 0.25. Uncorrelated relaxed molecular clock with a log-normal distribution was run on BEAST2 (62) under the Yule speciation process (53) and calibrated using the following time points: Acropora, 55 My; Dendrophyllidae, 127 My; Poritidae/Dendrophyllidae, 130 My; Agariciidae, 220 My; and Pocilloporidae, 70 My. Normal distribution was selected for each calibration point with an SD of 10%. For this analysis, the same model of nucleotide substitution was used in two separated runs, each with 10,000,000 generations saved every 10,000. The first 300 generations from each run were discarded as burn-in, and the remaining generations from each run were combined using LogCombiner version 1.10.4. The root from the recovered topology/molecular clock estimates was scaled to 470 My.

**Data Availability.** Mitogenome sequences data have been deposited in GenBank (MT409109). All other study data are included in the article text and supporting information.

**ACKNOWLEDGMENTS.** This work was funded in part by the National Science Centre (Poland) research grant 2017/25/BST10/02221 to J.S. and by a European Research Council Advanced Grant number 788752 (UltraPal) to A.M. M.V.K. is supported by the São Paulo Research Foundation (Fundação de Amparo à Pesquisa do Estado de São Paulo 2014/13123-2 and 2017/05229-5) and a CNPq Research Grant (Conselho Nacional de Desenvolvimento Científico e Tecnológico 301436/2018-5). I.L.R., J.C.H., and M.L.T. were supported by the UK Natural Environment Research Council NE/R005117/1. The RSS James Clark Ross JR15065 cruise was part of the Biodiversity, Evolution, and Adaptation team of the Environment and Evolution Programme at British Antarctic Survey. Funding of the mitogenome of *P. antarcticus* was provided by the NSF (1457817 to C.S.M. and 1457581 to E. Rodríguez). The work was also partially supported by the European Union within the European Regional Development Fund, through the Innovative Economy Operational Program POIG.02.02.00-05-025/09 (NanFun).

**Stolarski et al.** PNAS Latest Articles | 7 of 8

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