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## Evolution of the early Antarctic ice ages

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24 **Abstract**

25 Understanding the stability of the early Antarctic ice cap in the geological past is of  
26 societal interest because present-day atmospheric CO<sub>2</sub> concentrations have reached  
27 values comparable to those estimated for the Oligocene and the early Miocene epochs.  
28 Here we analyze a new high-resolution deep-sea oxygen isotope ( $\delta^{18}\text{O}$ ) record from the  
29 South Atlantic Ocean spanning an interval between 30.1 and 17.1 Myr ago. The record  
30 displays major oscillations in deep-sea temperature and Antarctic ice volume in response  
31 to the  $\sim 110$ -kyr eccentricity-modulation of precession. Conservative minimum ice  
32 volume estimates show that waxing and waning of at least  $\sim 85$  to 110% the volume of the  
33 present East Antarctic Ice Sheet is required to explain many of the  $\sim 110$ -kyr cycles.  
34 Antarctic ice sheets were typically largest during repeated glacial cycles of the 'mid'  
35 Oligocene ( $\sim 28.0$  to  $\sim 26.3$  Myr ago) and across the Oligocene-Miocene Transition ( $\sim 23.0$   
36 Myr ago). Yet, the high-amplitude glacial-interglacial cycles of the 'mid' Oligocene are  
37 highly symmetrical, indicating a more direct response to eccentricity-modulated  
38 precession than their early Miocene counterparts – which are distinctly asymmetrical.  
39 This analysis indicates that the relationship between cycle symmetry and continental ice  
40 volume is less straightforward than interpreted from late Pleistocene records. The long-  
41 term Oligo-Miocene increase in the asymmetry of the  $\sim 110$  kyr  $\delta^{18}\text{O}$  cycle culminated  
42 between  $\sim 23.0$  and 17.1 Myr ago in distinctly sawtooth-shaped glacial cycles – indicative  
43 of prolonged ice build up and delayed, but rapid, glacial terminations. We hypothesize  
44 that the long-term transition to a warmer climate state with sawtoothed shaped glacial  
45 cycles in the early Miocene was brought about by subsidence and glacial erosion in West  
46 Antarctica during the late Oligocene and/or a change in the variability of atmospheric

47 CO<sub>2</sub> levels on astronomical time scales that is not yet captured in existing proxy  
48 reconstructions.

49

50 **Keywords**

51 Unipolar icehouse, early Antarctic ice sheet, Oligocene-Miocene, glacial-interglacial  
52 cycle geometries.

53

54 **Significance**

55 The Antarctic ice cap waxed and waned on astronomical time scales throughout the  
56 Oligo-Miocene time interval. We quantify geometries of Antarctic ice age cycles, as  
57 expressed in a new climate record from the South Atlantic Ocean, to track changing  
58 dynamics of the unipolar icehouse climate state. We document numerous ~110-thousand  
59 year long oscillations between a near-fully glaciated and deglaciated Antarctica that  
60 transitioned from being symmetric in the Oligocene to asymmetric in the Miocene. We  
61 infer that distinctly asymmetric ice age cycles are not unique to the late Pleistocene or to  
62 extremely large continental ice sheets. The patterns of long-term change in Antarctic  
63 climate interpreted from this record are not readily reconciled with existing CO<sub>2</sub> records.

64

65 Author contributions: D.L., H.M.B., M.J.M.S., and A.E.D. generated the data. D.L. and  
66 A.T.M.B. performed the statistical analyses. D.L., A.T.M.B., P.A.W., and S.M.B. wrote  
67 the manuscript. All authors designed the study, discussed the results and commented on  
68 the manuscript.

69

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## 74 **Introduction**

75 The early icehouse world of the Oligocene and early Miocene epochs (hereafter referred  
76 to as Oligo-Miocene) is bracketed by two major climate events: the Eocene-Oligocene  
77 Climate Transition (~34 Myr ago, EOT) and the onset of the Middle Miocene Climatic  
78 Optimum (~17 Myr ago) (1). Deep-sea proxy records and sedimentological evidence  
79 from the Antarctic continental shelves indicate the expansion of continental-size ice  
80 sheets on Antarctica at the EOT (2, 3), and sedimentary records from the western Ross  
81 Sea on the East Antarctic margin document large subsequent oscillations in ice-sheet  
82 extent on astronomical time scales during the Oligo-Miocene (4). In contrast, large ice  
83 sheets did not develop in the high northern latitudes until the late Pliocene (5). Thus, the  
84 Oligo-Miocene presents an opportunity to study the dynamics of a unipolar (Antarctic)  
85 icehouse climate state without the overprint of Northern Hemisphere ice sheets on  
86 benthic foraminiferal  $\delta^{18}\text{O}$  records. Published proxy records of atmospheric  $\text{CO}_2$   
87 concentration show a decline from the Oligocene to the Miocene (6, 7) that is broadly  
88 contemporaneous with a strong minimum in the ~2.4 Myr eccentricity cycle at ~24 Myr  
89 ago (8), which would promote continental ice sheet expansion if radiative forcing was the  
90 dominant control on ice volume. Previous studies using drill-core records from the deep  
91 ocean demonstrate a climatic response to astronomical forcing for the Oligocene (9) and  
92 parts of the Miocene (10-12). Yet to improve understanding of the behavior of the

93 climate/cryosphere system we need longer high-resolution records from strategic  
94 locations that capture the changing response of the high latitudes to the combined effects  
95 of CO<sub>2</sub>, astronomical forcing and tectonic boundary conditions.

96

#### 97 **Walvis Ridge Ocean Drilling Program Site 1264**

98 To shed new light on southern high-latitude climate variability through the Oligo-  
99 Miocene, we analyze a new high-resolution benthic foraminiferal  $\delta^{18}\text{O}$  record from  
100 Walvis Ridge, located in the southeastern Atlantic Ocean (Ocean Drilling Program Site  
101 1264; 2505 m water depth; 2000–2200 m paleo-water depth; 28.53°S, 2.85°E, Fig. 1; (13,  
102 14)). An astrochronology for Site 1264 was developed by tuning CaCO<sub>3</sub> estimates to the  
103 stable eccentricity solution independently of the benthic  $\delta^{18}\text{O}$  record (14). On the  
104 eccentricity-tuned age model, the Site 1264 record spans a 13-Myr time window between  
105 30.1 and 17.1 Myr ago and ranges between 405-kyr Eccentricity Cycles 74–43 and ~2.4-  
106 Myr Eccentricity Cycles 13–8 (Fig. 1; (14)), representing the first continuous record from  
107 a single site spanning the 'mid' Oligocene to early Miocene. Five distinct time intervals  
108 with clear multi-Myr climatic trends are identified in this new  $\delta^{18}\text{O}$  dataset from Walvis  
109 Ridge: (i) an early Oligocene time interval of climate deterioration (~30.1–28.0 Myr  
110 ago); (ii) a generally cold but highly unstable mid-Oligocene time interval (~28.0–26.3  
111 Myr ago), which we refer to as the Mid Oligocene Glacial Interval (MOGI); (iii) a late  
112 Oligocene time interval characterized by low-amplitude climate variability and stepwise  
113 climatic amelioration (~26.3–23.7 Myr ago), confirming that this warming trend is a real  
114 feature of Cenozoic climate history (9) rather than an artifact of composite records from  
115 multiple sites in different ocean basins; (iv) a time interval of persistently high-amplitude

116 climate variability spanning the Oligocene-Miocene Transition (OMT) and the earliest  
117 Miocene (~23.7–20.4 Myr ago); and (v) a time interval of moderate-amplitude climate  
118 variability during the latter part of the early Miocene (~20.4–17.1 Myr ago).

119

120 Following the MOGI, the late Oligocene warming phase proceeded in a series of three  
121 distinct steps (~26.3, ~25.5, and ~24.2 Myr ago), with the peak warming/lowest ice  
122 volume confined to a ~500 kyr period (~24.2–23.7 Myr ago). This climate state was  
123 terminated by the OMT, which consists of two rapid ~0.5‰ increases in benthic  $\delta^{18}\text{O}$   
124 that are separated by an interval (405-kyr eccentricity cycle long) of partial  $\delta^{18}\text{O}$  recovery  
125 (14). The onset of the OMT is thereby comparable in structure to the EOT (3). A 405-kyr  
126 long overall decrease in benthic  $\delta^{18}\text{O}$  marks the recovery phase of the OMT.

127

### 128 **Ice volume estimates**

129 To better understand the significance of the documented  $\delta^{18}\text{O}$  variability on long-term  
130 change in the high-latitude climate system, we make a conservative estimate of the  
131 minimum contribution of continental ice volume to the Site 1264 benthic  $\delta^{18}\text{O}$  signal by  
132 assuming that Oligo-Miocene bottom-water temperatures at Site 1264 were never colder  
133 than the current temperature of 2.5°C and applying an average  $\delta^{18}\text{O}$  composition of  
134 Oligo-Miocene ice sheets ( $\delta^{18}\text{O}_{\text{ice}}$ ) of -42‰ VSMOW (see Methods; (15)). These  
135 minimum ice volume estimates (Fig. 1) are consistent with estimates of glacioeustatic sea  
136 level change from the New Jersey shelf (16) and those generated by inverse models of  
137 multi-site composite  $\delta^{18}\text{O}$  records (17). These ice volume estimates and sea level

138 reconstructions strongly suggest that a very large part of the benthic  $\delta^{18}\text{O}$  signal is linked  
139 to large ice volume changes on Antarctica.

140

141 Three major new results stand out in the minimum ice-volume calculations on the Site  
142 1264 benthic  $\delta^{18}\text{O}$  record (Fig. 1A). First, excluding the OMT interval, the Oligocene  
143 glacials are characterized by larger continental ice-sheet volumes than those of the early  
144 Miocene, particularly during the MOGI between  $\sim 28.0$  and  $26.3$  Ma. Second, across the  
145 OMT, Antarctica transitioned from a climate state that was fully deglaciated to one  
146 characterized by an ice sheet as large as the present East Antarctic Ice Sheet and back  
147 into a fully deglaciated state in less than 1 Myr. Third, many glacial-interglacial cycles in  
148 the benthic  $\delta^{18}\text{O}$  record are associated with a  $\delta^{18}\text{O}_{\text{sw}}$  change of at least  $\sim 0.60$  to  $0.75\text{‰}$ ,  
149 requiring the waxing and waning of  $\sim 21$  to  $26 \times 10^6 \text{ km}^3$  of ice, or  $\sim 85$  to  $110\%$  of present  
150 East Antarctic ice volume, on timescales of  $\leq 110$  kyr.

151

### 152 **Sinusoidal glacial-interglacial cycle properties**

153 The 13 Myr-long Oligo-Miocene benthic  $\delta^{18}\text{O}$  record from Site 1264 shows distinct  
154 cyclicity on astronomical time scales. Wavelet analysis reveals (Figs. 1, S1; (14)) that the  
155 amplitude of variability at the  $\sim 110$ -kyr eccentricity periodicity is particularly  
156 pronounced ( $\geq 1.0\text{‰}$  across the larger  $\delta^{18}\text{O}$  cycles). The amplitude of the 40-kyr obliquity  
157 periodicity is subdued in comparison to published records from other sites, presumably  
158 because of the higher sedimentation rates at those sites (12, 18). Four relatively short  
159 (405 kyr-long) intervals with particularly strong  $\sim 110$ -kyr-paced  $\delta^{18}\text{O}$  variability are also  
160 identified in the record (vertical gray bars, Fig. 1), demonstrating a pronounced climate-

161 cryosphere response to eccentricity-modulated precession of Earth's spin-axis (14). These  
162 intervals are contemporaneous with 405-kyr eccentricity maxima during ~2.4-Myr  
163 eccentricity maxima, specifically 405-kyr Cycles 73, 68, 57 and 49. Thus, while the OMT  
164 deserves its status as a major transient Cenozoic event (1, 19) because it is a prominent  
165 but transient glacial episode that abruptly terminates late Oligocene warming, the  
166 amplitude of ice age cycles observed as the climate system emerges from peak glacial  
167 OMT conditions is not unique in the Oligo-Miocene. In fact, this recovery phase of the  
168 OMT is one of four Oligo-Miocene intervals characterized by particularly high-amplitude  
169 ~110-kyr oscillations between glacial and interglacial Antarctic conditions (Fig. 1A). The  
170 record from Site 1264 is the first to unequivocally show that the ~2.4-Myr eccentricity  
171 cycle paces recurrent episodes of high-amplitude ~110-kyr variability in benthic  $\delta^{18}\text{O}$  (9,  
172 18) and provides a new global climatic context in which to understand Oligo-Miocene  
173 glacial history, carbon cycling (9, 20), mid-latitude terrestrial water balance (21) and  
174 mammal turnover rates (22) that show similar pacing. The intervals with particularly  
175 strong ~110-kyr cycles are separated by prolonged periods of attenuated ~110-kyr cycle  
176 amplitude, indicating that not all ~2.4-Myr and 405-kyr eccentricity maxima trigger  
177 similar cryospheric responses (Fig. 1). Specifically, ~2.4-Myr Eccentricity Cycle 11 in  
178 the late Oligocene is not characterized by high-amplitude ~110-kyr cycles (Fig. 1).  
179 Furthermore, no consistent relationship is found between strong ~110-kyr cycles in  
180 benthic  $\delta^{18}\text{O}$  and the ~1.2-Myr amplitude modulation of obliquity (14). This suggests that  
181 some other factor or combination of factors is responsible for the changing response of  
182 the climate system to astronomical forcing on ~110-kyr time scales over the Oligo-  
183 Miocene.

184

185 We assess the phase-relationships of the tuned  $\delta^{18}\text{O}$  data with respect to the main  
186 frequencies of orbital eccentricity to track the response times of the Oligo-Miocene  
187 climate system (Figs. 1, S2, S3). The benthic  $\delta^{18}\text{O}$  record from Site 1264 displays a  
188 marked multi-Myr evolution in the phasing of the  $\sim 110$ -kyr cycle relative to eccentricity  
189 starting with a  $\sim 10$  kyr phase lag during the mid Oligocene, followed by an unstable  
190 phase relation at  $\sim 26$  Myr ago and a steady increase in phase that culminates in a  $10$ – $15$   
191 kyr lag at  $\sim 19.0$  Myr ago (Fig. S3). This phase evolution is non-uniform for the  $\sim 95$ -kyr  
192 and  $\sim 125$ -kyr frequencies. On the basis of these data alone, we cannot rule out the  
193 possibility that part of the observed structure in the long-term phase evolution arises from  
194 changes in the proportional contribution of temperature and ice volume to benthic  $\delta^{18}\text{O}$   
195 (23). Yet the observed changes in phase are so large ( $\sim -10$  kyr to  $+15$  kyr) that changes  
196 in the response time of Antarctic ice sheets are most likely responsible; large continental  
197 ice sheets are the slowest-responding physical component of Earth's climate system and  
198 the only mechanism capable of inducing phase lags in deep-sea benthic  $\delta^{18}\text{O}$  records of  
199  $\sim 10$ – $15$  kyr (24). Analysis of phasing suggests that over full glacial-interglacial cycles,  
200 the high latitude climate–Antarctic ice sheet system responded more slowly to  
201 astronomical pacing during the MOGI ( $\sim 28.0$ – $26.3$  Myr ago) and early Miocene ( $\lesssim 23$   
202 Myr ago), than during either the early Oligocene ( $\sim 30.1$ – $28.0$  Myr ago) or late Oligocene  
203 ( $\sim 26.3$ – $23.7$  Myr ago).

204

205 **Bispectral analysis**

206 To investigate phase coupling between (astronomical) cycles embedded in the Site 1264  
207 benthic  $\delta^{18}\text{O}$  record, we apply bispectral techniques (25-27). A bispectrum identifies  
208 phase-couplings between three frequencies:  $f_1, f_2$  and their sum frequency  $f_1 + f_2 = f_3$ .  
209 When phase coupled, energy transfers nonlinearly between these frequencies and is  
210 redistributed over the spectrum. This results in lower and higher harmonics and in the  
211 formation of skewed and/or asymmetric cycle geometries such as those observed in the  
212  $\delta^{18}\text{O}$  record. We compare bispectra for two selected time intervals with strong  $\sim 110$ -kyr  
213 cyclicity (Fig. 2): a mid-Oligocene interval, during  $\sim 2.4$ -Myr Eccentricity Cycle 12  
214 (28.30–26.30 Myr ago), and an OMT-spanning interval, during  $\sim 2.4$ -Myr Eccentricity  
215 Cycle 10 (23.54–21.54 Myr ago). A third, early Miocene example is considered in Fig.  
216 S5. The bispectra show that during both the mid-Oligocene and the OMT numerous  
217 phase-couplings occur with frequencies that include, but are not limited to, astronomical  
218 cycles. Most interactions occur between cycles with periodicities close to those of  
219 eccentricity (periods of 405,  $\sim 125$  and  $\sim 95$  kyr/cycle, equal to frequencies of 2.5, 8.0 and  
220 10.5 cycles/Myr respectively) that exchange energy among one another and also with  
221 higher frequencies. The close proximity of both positive and negative interactions around  
222 eccentricity frequencies (Figs. 2, S4) suggests that these frequencies redistribute energy  
223 by broadening spectral peaks in  $\delta^{18}\text{O}$ . This process may explain the observed  $\sim 200$ -kyr  
224 cycle (Fig. 1; (14)). The main difference between the two selected time intervals is that  
225 the OMT bispectrum reveals many more nonlinear interactions (Fig. 2), both positive and  
226 negative, which indicates that the climate/cryosphere system responded in a more  
227 complex and indirect manner to insolation forcing across the OMT than during the  
228 MOGI. This observation may point to the activation of heightened positive feedback

229 mechanisms across the OMT related to continental ice-sheet growth and decay (12, 28),  
230 possibly involving the carbon cycle (29) or Antarctic sea ice (30).

231

### 232 **Non-sinusoidal glacial-interglacial cycle properties**

233 To further understand the nonlinearity in the climate system documented by the bispectra,  
234 we assess non-sinusoidal (i.e. non-Gaussian) cycle properties (Figs. 3, S5–S8, see also SI  
235 Text). Nonlinearity in climate cycles can be quantified in terms of skewness, asymmetry  
236 and kurtosis using standard and higher-order spectral analyses to elucidate the rapidity of  
237 climatic transitions (see Methods). The remarkably consistent negative skewness in the  
238  $\delta^{18}\text{O}$  record (mean  $-0.18$ , Figs. 3, S8) indicates that Oligo-Miocene glacials were longer  
239 in duration than interglacials – a result that is consistent with the late Pleistocene record  
240 (Fig. S6; (26, 27, 31)). To assess the time spent per cycle in full glacial and full  
241 interglacial conditions (in contrast to skewness which records the duration of glacials  
242 versus interglacials), we also calculate the evolution of cycle kurtosis through the benthic  
243  $\delta^{18}\text{O}$  record. Square-waved (platykurtic) glacial-interglacial cycles are more evident in  
244 the Site 1264 record than thin-peaked (leptokurtic) ones, apart from an early Miocene  
245 interval between  $\sim 21.5$  and  $19.0$  Myr ago when leptokurtic cycles prevail (Figs. 3, S8).  
246 This observation indicates that the Oligo-Miocene climate system generally favored full  
247 glacial and full interglacial conditions and transitioned rapidly between those two climate  
248 states. We attribute this finding to the operation of well-documented strong positive  
249 feedbacks on ice sheet growth and decay (24, 28).

250

251 To understand the relative rates of ice sheet growth versus decay we quantify cycle  
252 asymmetry. While the Site 1264 record shows consistently skewed Oligo-Miocene ~110-  
253 kyr glacial-interglacial cycles, we document a major change over time in the symmetry of  
254 those cycles that is marked by a transition to more asymmetric cycles which began ~23  
255 Myr ago at the OMT. This change represents a shift to a new climatic state characterized  
256 by strong ~2.4-Myr pacing of glacial-interglacial asymmetry and is associated with lower  
257 atmospheric CO<sub>2</sub> levels (Fig. 3; (6, 7)) Asymmetry in the data series is particularly  
258 pronounced during 405-kyr Eccentricity Cycles 57 and 49 (at ~22.7 and 19.5 Myr ago),  
259 which are characterized by distinctly sawtooth-shaped ~110-kyr cycles, suggesting a  
260 causal link between cycle amplitude and asymmetry during the early Miocene, but not  
261 during the MOGI. The distinctly asymmetric cycles suggest that the early Miocene  
262 Antarctic ice sheets periodically underwent intervals of growth that were prolonged  
263 relative to astronomical forcing and then underwent subsequent rapid retreat in a manner  
264 akin to the glacial terminations of the late Pleistocene glaciations, in which the large ice  
265 sheets of the Northern Hemisphere were major participants (26, 27, 31). The highly  
266 asymmetric (sawtooth) nature of late Pleistocene glacial-interglacial cycles is thought to  
267 originate from a positive ice mass-balance that persists through several precession- and  
268 obliquity-paced summer insolation maxima. This results in decreased ice-sheet stability  
269 and rapid terminations every ~110 kyr, once the ablation of the Northern Hemisphere ice  
270 sheets increases dramatically in response to the next insolation maximum. The increase in  
271 ablation is caused by lowered surface elevation of the ice sheets resulting from crustal  
272 sinking and delayed isostatic rebound (32). Similar mechanisms are implied for the large  
273 Antarctic ice sheets of the OMT (~22.5 Myr ago) but it is less clear why the smaller ice

274 sheets of the early Miocene (~19.5 Myr ago) would exhibit this distinctly sawtoothed  
275 pattern of growth and decay (Fig. 3).

276

### 277 **Climate–cryosphere evolution**

278 Analysis of the new  $\delta^{18}\text{O}$  record from Site 1264 raises two important questions: (i) Why  
279 did Antarctic ice sheets decrease in size after the OMT? (ii) Why was hysteresis (i.e.,  
280 glacial-interglacial asymmetry) apparently stronger for both the large OMT and the  
281 smaller early Miocene ice sheets than for the large ice sheets of the Oligocene? One  
282 explanation for the long-term change in ice volume is that the large glacial ice volumes of  
283 the MOGI were possible because of higher topography in West Antarctica (33) that  
284 permitted formation of a large terrestrial ice sheet that also buttressed growth of ice  
285 sheets on East Antarctica (24, 34). In this interpretation, tectonic subsidence and glacial  
286 erosion during the late Oligocene caused a shift to a smaller marine-based ice sheet in  
287 West Antarctica (24, 34), which limited the maximum size of the early Miocene Antarctic  
288 ice sheets during peak glacial intervals.

289

290 The early Miocene ice sheets may have been less responsive to astronomically paced  
291 changes in radiative forcing because of colder polar temperatures under lower  $\text{CO}_2$   
292 conditions from ~24 Myr ago onwards (7) or restriction of ice sheets to regions of East  
293 Antarctica above sea level following the late Oligocene subsidence of West Antarctica  
294 (24, 34). Another possibility is that the large ice sheets that characterized the peak  
295 glacials of the MOGI underwent rapid major growth and decay because of higher-  
296 amplitude glacial-interglacial  $\text{CO}_2$  changes than during the early Miocene. Such

297 hypothesized high amplitude changes in CO<sub>2</sub> would have had a direct effect on radiative  
298 forcing, which in turn would have caused faster feedbacks and a more linear response to  
299 eccentricity modulated precession. Given that larger ice volumes are to be expected in a  
300 climatic state that is characterized by high cycle asymmetry and low atmospheric CO<sub>2</sub>  
301 concentration, a third possibility is that the conservative calculations substantially  
302 underestimate true ice volumes for the early Miocene. Each of these hypotheses can be  
303 tested through a combination of scientific drilling on the West Antarctic shelf margin and  
304 development of high-resolution CO<sub>2</sub> and marine temperature proxy records with  
305 astronomical age control. We predict that strong eccentricity-driven CO<sub>2</sub> cycles (~110,  
306 405, & ~2400 kyr) that are closely in-step with ice volume changes will emerge in proxy  
307 CO<sub>2</sub> reconstructions for the Oligo-Miocene time interval. Assuming that changes in  
308 partitioning of the benthic δ<sup>18</sup>O signal between temperature and ice volume are modest  
309 throughout the Oligo-Miocene, the deep-sea δ<sup>18</sup>O record from Site 1264 suggests a clear  
310 long-term shift from a more glacial Oligocene to a less glacial early Miocene climate  
311 state – a pattern of change not readily reconciled with the long-term decrease in published  
312 CO<sub>2</sub> records.

313

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323

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457

### 458 **Figure Legends**

459 **Fig. 1. High-latitude climate/cryosphere evolution during the Oligo-Miocene and**  
460 **sinusoidal glacial-interglacial cycle properties.** (A) Benthic foraminiferal (*Cibicides*  
461 *mundulus*)  $\delta^{18}\text{O}$  record from ODP Site 1264 (gray line; (14)) and SiZer smooth (blue line,  
462 see Methods). Minimum ice volume contribution (lilac area, right axis) to the benthic  
463  $\delta^{18}\text{O}$  record calculated relative to all values exceeding 1.65‰ (left axis, see Methods).  
464 Dashed red line represents the contribution to benthic  $\delta^{18}\text{O}$  of a present day-sized East  
465 Antarctic Ice Sheet ( $\delta^{18}\text{O}_{\text{ice}} = -42\text{‰}$ ). (B–D) Sinusoidal glacial-interglacial cycle  
466 properties. (B) Wavelet analysis of the Site 1264 benthic  $\delta^{18}\text{O}$  record. White dashed lines  
467 represent the ~95- and ~125-kyr eccentricity periodicities, respectively. (C) Filter of the  
468 Site 1264 benthic  $\delta^{18}\text{O}$  record centered around the ~110-kyr periodicity (dark blue line)  
469 and its amplitude modulation (light blue line and area), compared to those of eccentricity  
470 (gray lines and area). The filter values are proportional to the eccentricity (left axis) and  
471 the VPDB scale (right axis), respectively. In the background (light brown line and area)  
472 the ~2.4-Myr component of Earth's orbital eccentricity is shown (+0.02, brown bold italic  
473 numbers). (D) Phase-evolution of the ~125-kyr (dark blue area, green dots) ~95-kyr  
474 (purple area, brown dots) and combined (including intermediate frequencies) ~110-kyr

475 (light blue area, orange dots) cycle to eccentricity, which show independent evolutions.  
476 Vertical gray bars represent 405-kyr Eccentricity Cycles 49, 57, 68 and 73 (dark gray  
477 italic numbers), characterized by exceptionally strong  $\sim 110$ -kyr responses in benthic  $\delta^{18}\text{O}$   
478 (Fig. 3; (14)).

479

480 **Fig. 2. Bispectra assessing phase coupling and energy transfers between frequencies**  
481 **in the  $\delta^{18}\text{O}$  data.** Bispectral analyses on benthic  $\delta^{18}\text{O}$  across two, 2-Myr long windows  
482 with strong  $\sim 110$ -kyr cycles (see also Fig. S4). (A) Bispectrum across the OMT interval,  
483 during  $\sim 2.4$ -Myr Eccentricity Cycle 10 (23.54–21.54 Myr ago). (B) Bispectrum across  
484 the MOGI, during  $\sim 2.4$ -Myr Eccentricity Cycle 12 (28.30–26.30 Myr ago). The colors of  
485 the bispectrum show the direction of the energy transfers. The intensity of the colors is  
486 indicative of the magnitude of energy transfers (see Methods). Red indicates a transfer of  
487 spectral power from two frequencies  $f_1$  (see x-axes) and  $f_2$  (see y-axes), to frequency  $f_3$  ( $f_1$   
488  $+ f_2 = f_3$ ). In contrast, blue represents a gain of spectral power at frequencies  $f_1$  and  $f_2$ ,  
489 from frequency  $f_3$ . Gray lines reflect the main astronomical frequencies of eccentricity,  
490 obliquity and precession.

491

492 **Fig. 3. Non-sinusoidal glacial-interglacial cycle properties.** (A) Atmospheric  $\text{CO}_2$  data  
493 for the Oligo-Miocene and their long-term smooths (turquoise line and area, see  
494 Methods) through the reconstructed values and their maximum and minimum error  
495 estimates (black error bars). Gray diamonds represent phytoplankton  $\text{CO}_2$  estimates,  
496 yellow squares are based on stomata, and purple-red triangles represent  $\text{CO}_2$  estimates  
497 based on paleosols (6, 7). Multiplication factors on the right refer to pre-industrial (p.-i.)

498 CO<sub>2</sub> concentrations of 278 ppm. CE stands for Common Era. (B-E) Four 405-kyr long  
499 intervals with exceptionally strong ~110-kyr cycles in benthic  $\delta^{18}\text{O}$ , plotted against  
500 eccentricity and its ~2.4-Myr component (+0.02). These intervals occur during (B) the  
501 early Miocene, contemporaneous with 405-kyr Eccentricity Cycle 49, (C) the Oligo-  
502 Miocene transition, Cycle 57, (D) the mid-Oligocene, Cycle 68, and (E) the early  
503 Oligocene, Cycle 73 (white italic numbers). For panels (B-E) only: long ticks on the age-  
504 axis indicate 500 kyr steps and short ticks 100 kyr steps. (F-H) Non-sinusoidal glacial-  
505 interglacial cycle properties. (F) Skewness, (G) Asymmetry, and (H) Kurtosis of the Site  
506 1264 benthic  $\delta^{18}\text{O}$  record quantified over a 2-Myr long sliding window using standard  
507 (turquoise circles) and bispectral (purple-pink triangles) methods (see Methods). The  
508 colored areas indicate the  $2\sigma$  upper and lower ranges of asymmetry. (I) Earth's orbital  
509 eccentricity (8) and its ~2.4-Myr component (+0.02, brown bold italic). Vertical gray bars  
510 as in Fig. 1. To the right of panels F-H the corresponding cycle shapes are depicted and  
511 the direction of time is indicated; ig = interglacial, g = glacial.  
512