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基于银杏(*Ginkgo*)与水杉(*Metasequoia*)叶化石气孔指数的新生代大气CO_2浓度记录

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摘 要

大气CO_2浓度与地球气候变化有密切的关系，通过重建高精度、高分辨率的古大气CO_2浓度探索大气CO_2浓度与气候变化之间的关系是当今地质学、古生物学等领域研究的热点之一。银杏(*Ginkgo*)与水杉(*Metasequoia*)是两类广为人知的孑遗植物，其叶化石的气孔指数是重建新生代古大气CO_2浓度常用的代用指标。但是，不同学者的研究在气孔指数计数方法、古大气CO_2浓度转换等过程中的标准并不统一，导致重建的古大气CO_2浓度误差较大。因此，本研究对前人已发表的银杏和水杉叶化石的研究进行整理，共收集92个银杏和26个水杉叶片化石气孔指数数据，按照统一的方法重建新生代各个时期的大气CO_2浓度，并进一步探讨新生代大气CO_2浓度变化与古温度变化之间的关系。

关键词

气候变化，叶化石，气孔指数，新生代，银杏，水杉

Cenozoic CO_2 Concentration History Based on *Ginkgo* and *Metasequoia* Stomatal Index

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Abstract

The variation of atmospheric CO_2 concentration is believed closely related to the present global warming, and paleo-CO_2 reconstruction with high precision and high resolution has become one of the hot topics of geology and paleontology recently. *Ginkgo* and *Metasequoia* are two well-known

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relict taxa, whose leaf fossils are abundant throughout the Cenozoic era, and stomatal index of their leaf fossils is one of the most commonly used paleo-CO_2 proxies. However, different studies have different standards in stomatal index counting methods and paleo-atmospheric CO_2 concentration estimation methods, leading to large inconsistence in their results. In this study, previously published stomatal index data of 92 *Ginkgo* leaves and 26 *Metasequoia* leaves were collated, and then the atmospheric CO_2 concentration history of the Cenozoic were reconstructed. The relationship between the Cenozoic atmospheric CO_2 concentration and paleo-temperature was further discussed.

Keywords

Climate Change, Fossil Leaf, Stomata Index, Cenozoic, *Metasequoia*, *Ginkgo*

1. 引言

众所周知，二氧化碳(CO_2)作为大气中的主要温室气体，是引起当前全球变暖的罪魁祸首之一[1] [2] [3]。通过分析过去大气 CO_2 浓度变化与全球气候变化的相关关系，可以为解决全球气候变化问题提供理论基础。但是，目前有数据观测记录的大气 CO_2 历史还不足百年，因此高精度、高分辨率的古大气 CO_2 浓度数据对于深入理解当今的全球气候变化有着重要的意义。

目前，重建古大气 CO_2 浓度的方法主要包含以下三种：测定冰芯中储存的空气组成成分[4]，地球化学模型[5] [6] [7]和各种各样的古大气 CO_2 浓度的代用指标[8]。一般认为，直接测量冰芯中的空气组成所得到的古大气 CO_2 浓度最为可靠。但是，过于古老的冰芯会因为地热等因素而无法保存，因此，冰芯只能记录 0.8 Ma 以来的大气 CO_2 浓度[9]。地球化学模型是基于化学热力学或/和化学动力学原理重建古大气 CO_2 浓度，虽然该方法可以完整地重建约 600 Ma 以来的古大气 CO_2 浓度，但是难以将重建数据的时间分辨率控制在 5 Myr 以下，并且该方法也难以辨别甲烷(CH_4)在全球温度变化中所起的作用[5] [6] [7]。因此，为了弥补上述两种方法的局限性，同时验证其结果的准确性，许多研究利用各种类型的代用指标重建不同地质历史时期的古大气 CO_2 浓度[8]，如古土壤[10]、海洋浮游植物[11]、海洋浮游有孔虫化石[11]、植物化石碳同位素判别($\Delta^{13}C$) [12]以及叶化石的气孔频度(stomatal frequency)等。

根据材料的来源，这些代用指标可以分为两类——海洋性代理指标和陆地性代理指标，而叶化石的气孔频度是常用的陆地性古大气 CO_2 浓度代用指标之一。气孔频度方法具有时间精度高、重建 CO_2 浓度的准确度高、叶化石在地层中分布广泛易获取等优点，因而在重建古大气 CO_2 浓度的研究上具有不可或缺的优势[13] [14]。该方法的理论基础是陆生维管植物叶片的气孔频度与大气 CO_2 水平显著相关[15]。气孔频度包括气孔密度(stomatal density, SD)和气孔指数(stomatal index, *SI*) [16]：SD 为单位面积内包含气孔的数量(个数/mm^2)，*SI* 为气孔占表皮细胞总数的比例(%)。由于 *SI* 的计算不受叶面积变化和叶表皮细胞大小的影响，且温度、大气湿度和土壤水分供应等环境参数对 *SI* 的影响十分有限，因此一般认为 *SI* 比 SD 所提供的古大气 CO_2 浓度重建结果更为准确[17]。

目前为止，已有许多不同的植物化石被用于古大气 CO_2 浓度重建[18]-[32]，但是，由于气孔频度与大气 CO_2 浓度的关系具有高度的种间特异性[13]，所以应用气孔频度方法进行古大气 CO_2 浓度重建前必须先确定化石的现生种或最近现生亲缘种(nearest living relatives, NLRs)的气孔频度与大气 CO_2 浓度的相

关关系，而选择合适的植物类群可以极大程度地降低实验的难度并提高结果的准确度。银杏(*Ginkgo* biloba)与水杉(*Metasequoia* glyptostroboides)是两种广为人知的孑遗植物，这两个类群的化石储量丰富且遍布于北半球各地层[33]。[34]并且，由于银杏与水杉的形态学特征明显，因此在野外工作中易于辨认出其化石。根据文献记录，最古老的水杉化石被发现于晚白垩纪的早期[33]，而银杏的化石在整个中生代至新生代都十分丰富[34] [35]。根据形态学特征、生物化学和生理学特征等，银杏和水杉的化石种都可以被认定为现生种的同种或者最近亲缘种[36] [37] [38]。因此，相较于其它物种，银杏和水杉可以提供较长地质时期内连续的 CO_2 记录，是重建古大气 CO_2 的理想材料。

利用不同年代采集的腊叶标本和/或人工气候室 CO_2 浓度控制实验，银杏和水杉的气孔指数与大气 CO_2 浓度之间的函数关系已经确立[34] [36]，并且已经有许多研究利用银杏和水杉的叶片化石重建新生代和中生代的大气 CO_2 浓度[34] [35] [36] [37] [38]。但是，许多发表时间较早的银杏或者水杉叶化石的气孔指数并未被用于进行古大气 CO_2 浓度的重建[39] [40] [41] [42]，并且有些研究尽管根据银杏或者水杉叶片化石重建了古大气 CO_2 浓度，但是各个研究在气孔指数计数方法、古大气 CO_2 浓度转换等过程中的标准并不统一[22] [34]-[36] [43] [44]，而本研究旨在汇总整理已发表的新生代银杏和水杉叶化石的研究，对这些银杏和水杉叶化石的气孔指数进行统计，按照统一的方法重建新生代大气 CO_2 浓度，并探讨这一时期 CO_2 变化与温度变化的关系。

2. 材料与方法

本研究将对前人已发表的银杏和水杉叶化石的研究进行整理，共收集 92 个银杏叶片化石的气孔指数数据和 26 个水杉叶片化石气孔指数数据(附件 1)。由于植物叶片之间存在个体差异性，所使用化石叶片的数量会直接影响结果的准确性，为了避免这一现象，本研究在挑选数据时，会优先选择叶片数量大于 5 的数据。

虽然很多不同的研究曾发表过不同的水杉和银杏的气孔指数与大气 CO_2 浓度关系的函数关系式[22] [34]-[36] [43] [44]，但是截至目前为止，被引用次数最多的为 Royer、Wing [36]所发表的函数关系(公式 1 和公式 2)。因此，本研究将利用这两个函数关系式进行新生代古大气 CO_2 的重建。

银杏叶片 SI (%)与大气 CO_2 浓度(ppmv)之间的函数关系：

$$\text{大气CO}_2\text{浓度}(\text{ppmv}) = \frac{1-0.1564\times SI}{0.00374-0.0005485\times SI} \tag{1}$$

水杉叶片 SI (%)与大气 CO_2 浓度(ppmv)之间的函数关系：

$$\text{大气CO}_2\text{浓度}(\text{ppmv}) = \frac{SI-6.672}{0.003883\times SI-0.02897} \tag{2}$$

3. 结果

本研究的结果表明，银杏与水杉叶化石可以提供一个较为连续的新生代大气 CO_2 浓度变化记录(图 1；附件 1)。但是，在进行古大气 CO_2 重建的过程中发现，当银杏叶化石 SI 小于 6.9、水杉叶化石 SI 小于 7.6 时，古大气 CO_2 浓度的重建结果异常。因此，本研究在重建新生代大气 CO_2 浓度时剔除了 12 个会导致异常结果的 SI 数据(附件 1)。相较于银杏叶化石，水杉叶化石所能提供的数据量较小，尤其是在古新世，水杉叶片化石只提供了两个数据点。

根据银杏和水杉叶化石的气孔指数，新生代大气 CO_2 浓度在 277 ppmv~1024 ppmv 之间波动。其中，新生代大气 CO_2 浓度的最高记录出现在中始新世，而最低浓度的记录出现在更新世。整个新生代时期，大气 CO_2 浓度曾出现过三次峰值，分别位于古新世早期(约 60 Ma)，始新世中期(约 38 Ma)和中中新世(约

14 Ma) (图 1)。这三个时间点的大气 CO_2 浓度远远高于其它时期，达到了接近甚至超过 1000 ppmv 的水平。晚中新世之后，大气 CO_2 浓度开始逐渐下降，并最终达到与工业革命前相似的水平(约 270 ppmv)。

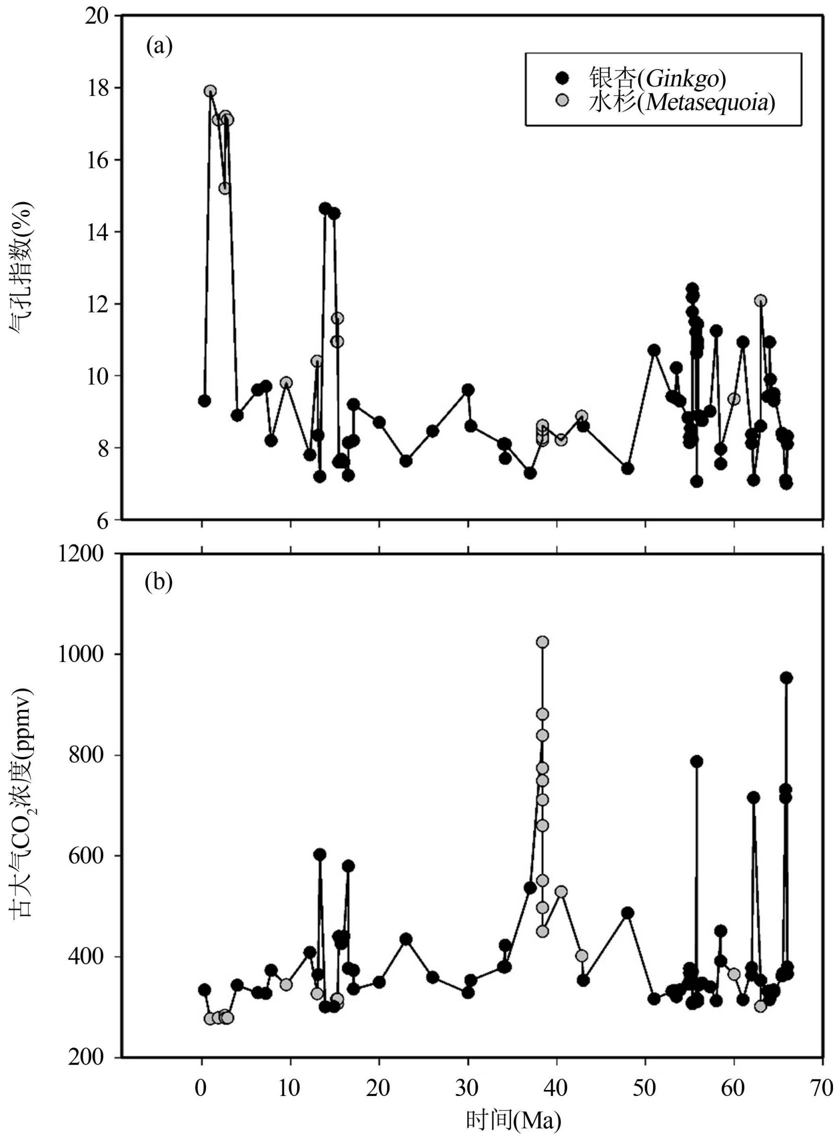

Figure 1. (a) The Cenozoic stomatal index (*SI*) of *Metasequoia* and *Ginkgo* leaves (Supplementary Table S1) and (b) the corresponding paleo-CO_2 concentration estimation
图 1. (a) 新生代各个时期水杉与银杏叶化石气孔指数(*SI*) (附件 1)及其(b) 对应的古大气 CO_2 浓度重建数据

4. 讨论

4.1. 不同植物对于气孔指数法的影响

除银杏与水杉的叶化石外，其它种类的木本植物叶化石的气孔指数也曾被用来重建新生代各个时期的大气 CO_2 浓度，例如，香蒲属(*Typha*) [18]、柳属(*Salix*) [19] [20] [21]、绿心樟属(*Ocotea*) [22]、桦木科桦木属(*Betula*) [23] [24] [25] [45]、栎属(*Quercus*) [26] [27] [28] [29]、月桂属(*Laurus*) [30]和水青冈属(*Fagus*) [31] [32]等等。然而，并不是所有植物的叶化石都适合作为古大气 CO_2 重建的材料。

首先，由于 C_4 植物在光合作用过程中将吸收的 CO_2 积累在维管束鞘内，外界大气 CO_2 浓度的变化对

C_4 植物的影响很小，因此其气孔频度对外界大气 CO_2 浓度的变化不敏感[46]，不可用于古大气 CO_2 重建。与 C_4 植物不同，C_3 植物吸收 CO_2 后将其固定于海绵组织和栅栏组织中，植物细胞内的 CO_2 浓度与外界大气 CO_2 浓度的比值一直保持在 0.7 左右[47] [48] [49]，因此 C_3 植物需要通过调节气孔的开闭和数量以应对大气 CO_2 浓度的变化。Royer [13]统计了 176 种 C_3 植物的气孔频度对 CO_2 浓度变化的响应情况，其中的大部分物种的气孔频度与大气 CO_2 浓度呈负相关关系。

尽管如此，许多叶片气孔频度对于大气 CO_2 变化敏感的 C_3 植物仍不能成为重建古大气 CO_2 的理想材料。这是由于气孔频度的精确统计依赖于化石角质层的完整性和清晰度，因此，那些角质层较薄的物种将极大程度地增加实验的操作难度。以银杏和水杉为例，相较于银杏叶化石，水杉叶化石所能提供的新生代大气 CO_2 浓度的数据量较小，尤其是在古新世，水杉叶片化石只提供了两个数据点[38] (图 1)。造成这一现象的一个重要原因是水杉叶片化石角质层较薄，在石化过程中不易保存。虽然也有一些水杉化石保存了较为完整的角质层，但是，这些角质层在实验过程中不易分离，分离后的角质层破损严重或者叶肉无法清理干净，给气孔频度的统计工作造成了困难[50]。此外，一些水杉叶片化石的角质层出现乳突或者鼓突结构[50]，这些结构会影响观察细胞边界，从而在一定程度上影响到气孔指数的统计，进而影响重建结果的准确性。

另外，植物的叶片由于出现了阳生叶与阴生叶的区别，且阳生叶与阴生叶对于大气 CO_2 浓度的响应程度是不同的，因此需要对化石叶片材料进行区分[28] [30] [31] [32]。有些物种如栎属植物，可以通过叶表皮细胞的形态加以区分[28] [30] [31] [32]，但是对于绝大多数木本双子叶植物来说，目前还没有可靠的方法可以有效地辨别出化石叶属于阳生叶还是阴生叶。此外，许多木本植物也存在雌雄异株的现象，例如银杏，虽然 Retallack [34]通过对比俄勒冈州的雌性和雄性银杏树叶的 *SI* 认为银杏的雌雄对于银杏的 *SI* 并没有显著性的影响，但是其它雌雄异株物种的 *SI* 是否存受到影响依旧存疑。

值得注意的是，在气孔指数法运用过程中还有一个容易被忽视的影响因素是化石叶片在埋藏前的搬运。有研究表明，生长在高海拔处的叶片在风、溪流等环境因素的作用下，垂直搬运距离可以大于 1000 米[32]。而大气 CO_2 分压会随着海拔的升高而降低，因此，海拔分布范围较广的物种，在叶片化石的 *SI* 统计中经常出现较大的变异幅度，远远超出个体差异性所能解释的范围[31] [32]。而这将导致重建出的 CO_2 结果偏低，降低了结果的准确性，而选择低海拔分布的物种则可以避免这一不确定性因素。

4.2. 与海洋有孔虫硼同位素古大气 CO_2 浓度记录对比

Beerling 和 Royer 曾比较不同代用指标重建出的新生代古大气 CO_2 数据，结果表明利用不同代用指标所重建的古近纪大气 CO_2 浓度数据间存在显著差异[8]。其中，海洋性代用指标中的海洋有孔虫硼同位素与本文所关注的陆地性代用指标叶化石气孔指数的结果差异最为显著[8]。虽然这两种方法都表明古大气 CO_2 浓度在新生代呈现出下降趋势(图 2)，但是，中新世之前，海洋有孔虫硼同位素的重建结果与叶化石气孔指数的结果间的差距十分明显，甚至在古新世早期硼同位素的重建结果比气孔指数法的重建结果高出大约 1000 ppmv [38] [43] [64]-[68]。银杏和水杉叶化石的气孔指数显示在古新世早期，中始新世和中中新世时期，大气 CO_2 浓度曾出现峰值[34] [43] [44] [68] [69]。虽然这些峰值也出现在海洋有孔虫硼同位素的记录中，但是海洋有孔虫硼同位素的重建结果是气孔指数法重建结果的两倍甚至更多，在早古新世至早始新世时期海洋有孔虫硼同位素所指示的 CO_2 浓度曾达到 2000 ppmv 以上[58] [59] [63] [67]。此外，古新世–始新世极热期(PETM；约 55 Ma)，海洋有孔虫硼同位素记录显示古 CO_2 浓度的范围为 1000 ppmv~2000 ppmv [64] [65] [66]，而银杏的气孔指数却表明该时期古大气 CO_2 浓度为 300 ppmv~350 ppmv [43]，甚至略低于当今的大气 CO_2 浓度水平。中新世以来，叶化石气孔指数的古大气 CO_2 重建结果与海洋有孔虫硼同位素的重建结果逐渐统一，两者结果间的差异缩小至 300 ppmv 之内。

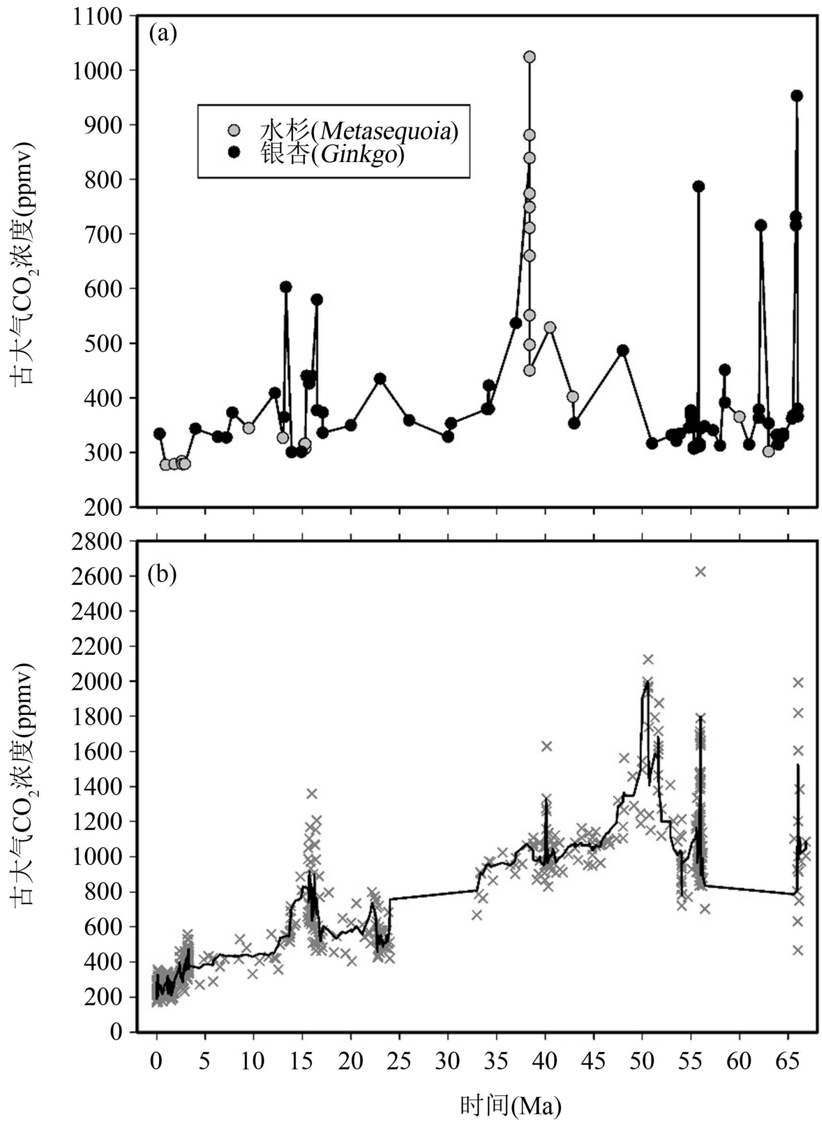

Figure 2. (a) The Cenozoic CO_2 concentrations recorded by *Ginkgo* and *Metasequoia* leaves (Supplementary Table S1) and (b) marine foraminifera [51]-[67]; the solid line in (b) indicates five-point moving average of the data.
图 2. (a) 新生代银杏与水杉叶化石大气 CO_2 浓度记录(附件 1)与(b) 海洋有孔虫硼同位素 CO_2 浓度记录[51]-[67]的对比；图(b)中的实线为五点移动平均值

造成海洋有孔虫硼同位素与叶化石气孔指数古大气 CO_2 重建结果间差异的原因可能包含以下两点。首先，Royer、Wing [36]建立银杏和水杉的气孔指数与大气 CO_2 浓度关系的函数关系式时所使用的材料包括 1856~2000 年间采集的蜡叶标本以及 350 ppmv 和 790 ppmv CO_2 浓度下温室栽培至少一个生长季的银杏和水杉叶片。因此，Royer、Wing [36]所使用的银杏和水杉的数据在 CO_2 浓度大于 350 ppmv 时并不连续，且数据量较小。此外，由于在高 CO_2 浓度下银杏和水杉气孔调节的灵敏度也有所下降，所以 Royer、Wing [36]认为其发表的模型在对于较高浓度的古大气 CO_2 (即较低的叶片化石 *SI*)重建的结果为半定量的。另一方面，有孔虫硼同位素方法重建的基本原理是利用海相碳酸盐岩硼同位素组成(δ^{11}B)与海水 pH 值的关系[70]，会受到成岩作用、海洋中硼同位素总量的变化、海洋总碱度等等因素的影响[71] [72]。古近纪时期海洋硼指标也倾向于比陆地硼指标指示更高的古大气 CO_2 浓度[72] [73] [74] [75]，因此推测海洋硼同位素结果有偏高的倾向。

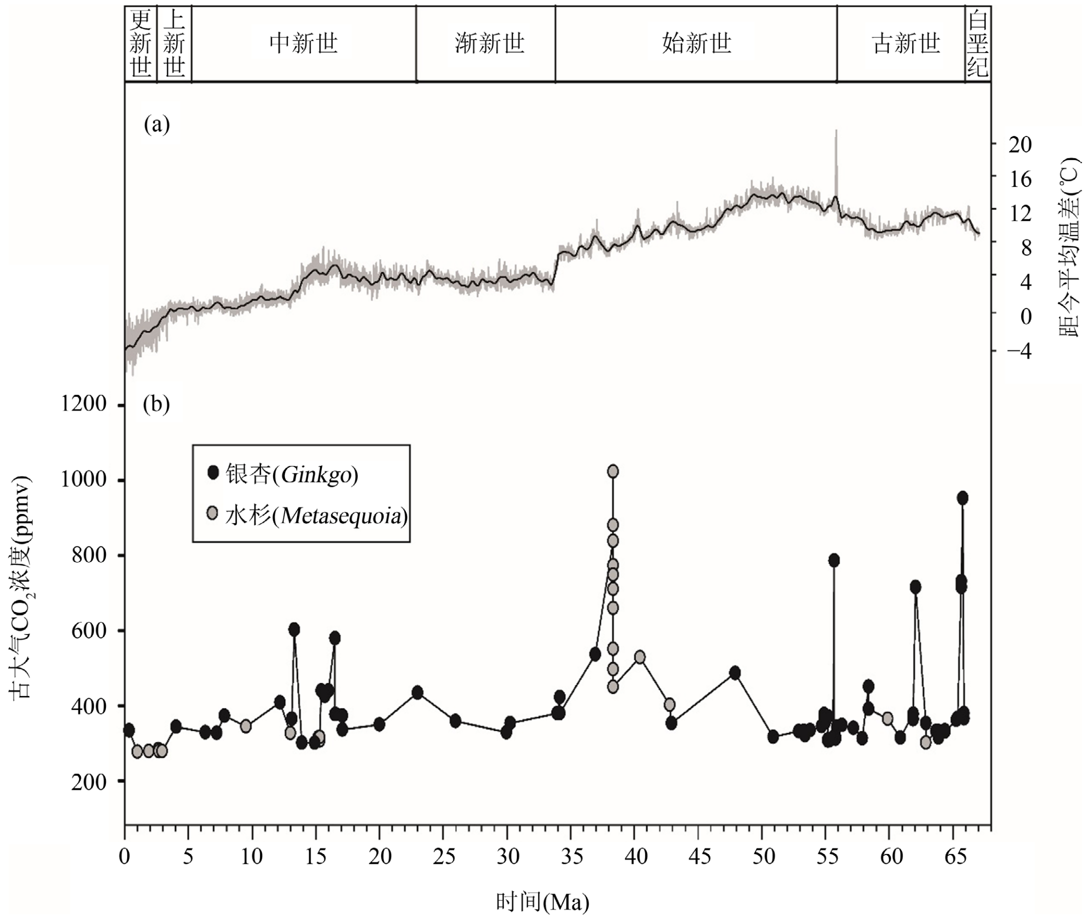

Figure 3. (b) Comparison between the Cenozoic atmospheric CO_2 concentration recorded by fossil *Ginkgo* and (a) *Metasequoia* leaves (Supplementary Table S1) with sea surface temperature records [76]

图 3. (b) 新生代银杏与水杉叶化石大气 CO_2 浓度记录(附件 1)与(a) 海面温度记录的对比[76]

4.3. 古大气 CO_2 浓度变化与古温度变化的关系

在新生代，地球经历了古新世和始新世的温暖时期，然后逐渐冷却，在上新世和更新世转变为冰室气候[76] [77]。从古新世至始新世早期，地表温度比现代高约 5℃~12℃ [76] [78]-[82] (图 3)，这一时期南北两极几乎没有冰盖覆盖[45]。古新世至始新世早期(约 65 Ma~50 Ma)高温环境的成因至今仍有争议，有些研究支持其主要归因于过高的大气 CO_2 浓度[64] [65] [66]，但是另一些研究则认为另一种温室气体甲烷的释放才是造成这一极端气候的罪魁祸首[38] [45] [83] [84] [85]。这一时期银杏叶片化石所记录的大气 CO_2 浓度变化范围较大，但是大多数银杏叶片所反映的大气 CO_2 浓度在 350 ppmv~450 ppmv 之间[43] [68]。并且 PETM 时期(约 55 Ma)，银杏叶片所指示的古大气 CO_2 浓度仅为 350 ppmv 左右[43]且该时期大多数银杏叶化石所记录的数据也在同一水平(图 3，附件 1)。相邻时期(60 Ma)采自美国阿拉斯加冰河湾的水杉化石叶片所记录的大气 CO_2 浓度为 365 ppmv [38]。根据本研究的结果，在古新世至始新世早期，气孔指数所反映的大气 CO_2 浓度与这一时期的温度并没有出现明显的耦合关系，因此从侧面支持其它因素，如甲烷等，是造成这一高温环境的主要因素。由于过去湿地的范围更广，甲烷可能是从湿地释放出来[85]，因此，早始新世大气中甲烷的含量迅速升高[86] [87]。并且，古新世晚期，由火山喷发引起的温室气体增加导致的海底相对快速的变暖也可能引发甲烷水合物的大规模释放[45]。而在这一时期，海洋有孔虫硼同位素所指示的大气 CO_2 浓度远远高于气孔指数重建的结果(见 4.2)，因此，与气孔指数法不同，这些基于

海洋有孔虫的古大气 CO_2 数据支持古新世至始新世早期(约 65 Ma~50 Ma)高温环境的主要成因是过高的大气 CO_2 浓度[58] [59] [63]-[67]。

自始新世早期开始，地球开始逐渐冷却，但在此过程中曾出现过两次地球温度的突然上升，即中始新世气候适宜期(MECO，约 40 Ma~40.5 Ma)和中中新世气候适宜期(MMCO, 17 Ma~15 Ma)。水杉和银杏叶化石记录显示中始新世和中中新世时期大气 CO_2 浓度分别为 401 ppmv~1024 ppmv [38] [69]和 306 ppmv~603 ppmv [34] [36] [52] [89]，并于 38.4 Ma [34] [89]和 13.3 Ma [34] [89]时出现大气 CO_2 浓度的峰值，与同一时期突升的海洋温度记录相对应，支持 MECO 和 MMCO 的气候暖期与大气 CO_2 浓度升高有关的观点[90] (图 3)。MECO 之后，银杏和水杉叶片的记录显示，大气 CO_2 浓度逐渐下降(图 2，附件 1)。始新世至中新世期间，两极冰盖开始形成，而逐渐降低的 CO_2 浓度可能是触发冰盖形成的原因之一[91] [92]。晚中新世至更新世时期，地球温度在不断下降，银杏和水杉的气孔指数所记录的大气 CO_2 浓度却在中新世极热期后至更新世时期从 350 ppm 左右逐渐下降至约 270 ppmv [37] [40] [41] [42]。虽然更新世与上新世的大气 CO_2 浓度之间存在显著差异，但大气 CO_2 浓度仅下降了不到 100 ppmv [37]。因此，有研究认为由于受到高纬度植被情况的差异等因素的影响，古气候对大气 CO_2 浓度的变化较如今更为敏感[93] [94]，因此大气 CO_2 浓度的微小改变也会显著影响地球温度变化趋势。此外，有研究认为中新世以来的气候变化不仅受到古大气 CO_2 浓度变化的影响，还受到季节性强弱和海洋环流变化的增加等其它因素的影响[95] [96] [97]，这些因素加速了中新世中晚期地球的冷却，同时也促进了大气 CO_2 浓度的减少。

5. 总结

利用银杏和水杉叶化石的气孔指数可以绘制出一条较为完整的新生代大气 CO_2 浓度历史曲线，但是渐新世至中中新世这一阶段目前数据较少，还需要进一步完善。银杏和水杉气孔指数记录的新生代大气 CO_2 浓度在 250 ppmv~1100 ppmv 之间波动，并于古新世早期、中始新世以及中中新世出现峰值。并且，新生代大气 CO_2 浓度的波动在古近纪十分剧烈，随后逐渐变弱，直至更新世时稳定在工业革命前的水平。通过与海面温度记录对比，银杏和水杉气孔指数所记录的古近纪大气 CO_2 浓度与温度之间的变化趋势并不一致。中新世以来大气 CO_2 浓度与地表温度都呈现下降趋势，但是相对于中新世以来地球的大幅度降温，大气 CO_2 浓度降低的幅度较小，因此认为当时的气候对大气 CO_2 浓度的变化较如今更为敏感。

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