

High resolution estimates of paleo-CO₂ levels through the Campanian (Late Cretaceous) based on *Ginkgo* cuticles

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ABSTRACT

Using the stomatal index technique, the Campanian (Late Cretaceous) atmospheric carbon dioxide levels are estimated based on a sequence of fossil cuticles of *Ginkgo adiantoides* (Ung.) Heer. *Ginkgo* cuticles were sampled from 11 beds in the Taipinglinchang Formation at Jiayin, Heilongjiang Province, northeast China. In general, the regression function based results show a gradual decrease of $p\text{CO}_2$ through Campanian with a background of $\sim 550\text{--}590$ ppm. The new data of the Campanian $p\text{CO}_2$ are more compatible with GEOCARB II model than those of GEOCARB III, although the new data have slightly higher values (30 ppm on average). A notable short-term carbon dioxide fluctuation (SCDF) is recognized in the upper Campanian (up to ~ 690 ppm), and is followed by a rapid return to background values of ~ 590 ppm.

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1. Introduction

Fossil cuticles provide unique insights into paleo-CO₂ ($p\text{CO}_2$) and terrestrial paleo-ecosystem changes throughout the Phanerozoic (Woodward, 1987; McElwain, 1998; Beerling and Royer, 2002a; Kürschner et al., 2008; Royer, 2008). A growing number of cuticle-based studies have attempted to estimate paleo-CO₂. The published data, however, indicate a significant range of values with little congruence not only compared to those derived from geochemical methods, but also among the paleobotanical approaches themselves (Yapp and Poths, 1992; Berner, 1997; McElwain et al., 1999; Retallack, 2001; Royer, 2001; Royer et al., 2001a; Tanner et al., 2001; Haworth et al., 2005). Paleobotanically, this inconsistency may be partly explained by multispecies analyses where different taxa show variable responses to CO₂ levels and CO₂ change. The monospecies-based $p\text{CO}_2$ estimates are, therefore, considered to be a more effective way to reduce the potential sources of error that arise through multi-species approaches.

It is likely that the monospecies-based CO₂ reconstruction can not be implemented for long periods of geological time, since no single species is available that survived throughout the history of

land plants with well-preserved cuticles. However, this solution is practical at least at the “age/stage” level of geological time. To date, most monospecies-based paleo-CO₂ estimations, which calibrate the stomatal indices (SIs) of fossil leaves to a modern reference set of the same species, are constrained to the latest Cretaceous and Cenozoic (e.g. Wagner et al., 1999; Royer et al., 2001b; Beerling et al., 2002; Kürschner et al., 2008). Few studies have quantitatively reconstructed the Late Cretaceous CO₂ based on the SIs of a monospecific sequence of fossil leaves.

This paper reports paleo-CO₂ estimates during the Campanian (Late Cretaceous) based on stomatal parameters from *Ginkgo adiantoides* (Ung.) Heer. The fossil *Ginkgo* leaves were collected from the Taipinglinchang Formation at Jiayin, Heilongjiang, northeast China (Fig. 1). We selected *Ginkgo* based on its ecological conservatism (Royer et al., 2003) and its apparent reliability as a paleo-CO₂ indicator shown through herbarium observations and plant experimentations (Chen et al., 2001; Royer, 2001; Sun et al., 2003). The present monospecies-based paleo-CO₂ estimates overcome the potential taxonomic bias imposed by multispecies studies.

2. Material and methods

2.1. Material

The *Ginkgo* fossils were collected from the Upper Cretaceous Taipinglinchang Formation along the right bank of Heilongjiang

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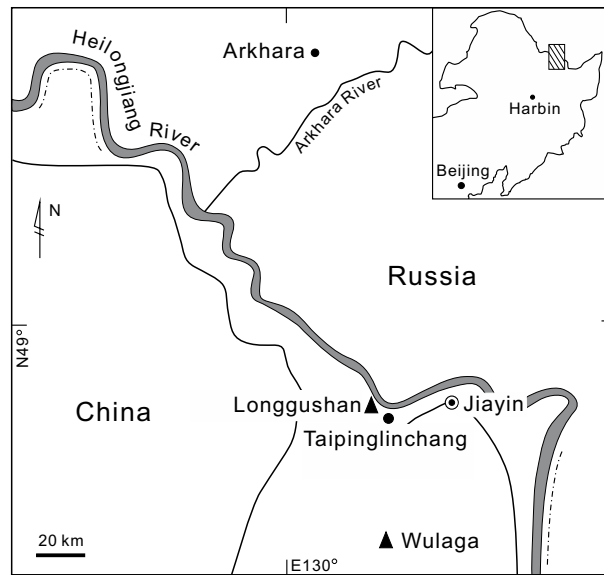


Fig. 1. Geographical position of *Ginkgo* fossil sites in Jiayin, Heilongjiang, NE China (solid triangle marks showing the sites within the Upper Cretaceous Taipinglinchang Formation).

River in Jiayin County, Heilongjiang, northeast China (Fig. 1), by the Research Team on the K-T boundary of Jilin University, during seven fieldworks since 2002. This plant-bearing formation represents a shallow lacustrine succession consisting of grey mudstone, siltstone and fine feldspathic sandstone (Fig. 2). It yields fossils of conchostacans, ostracods, fishes and plants. This formation is predominantly of Campanian age based on palynological data (Markevich et al., 2006; Sun et al., 2007b).

A total of 77 specimens of *G. adiantoides* with well-preserved cuticles were collected from 11 beds of the Upper Cretaceous Taipinglinchang Formation (Fig. 2). More than 5 leaves were sampled per bed except for beds 1 and 5. Although stomatal index (SI) measurements were made on fewer than five leaves for these two beds, we have included them here since no other species with cuticles were found in these stratigraphic levels.

2.2. Cuticle preparation and counting

For identification and stomatal analysis, the cuticle fragments of each *Ginkgo* specimen were treated by standard maceration for both SEM and LM (see Dilcher, 1974). The material was first identified by SEM, then the selected *G. adiantoides* specimens were photographed by LM.

For cuticle preparation, we selected the middle part of each *Ginkgo* leaf to obtain secure SI measurements, because stomatal parameters show less variability there than near the margins. At least three fragments were measured on each *G. adiantoides* leaf per bed; and stomatal counts were made on three or more intercostal fields per lower cuticle fragment as outlined by Poole and Kürschner (1999). In total, the counts were performed on 253 fragments from 77 specimens. The values reported here are averages of all measurements for each leaf at a particular bed.

The photographic instruments, JSM-6700F SEM and Olympus DP12 LM, were provided by the Research Center of Paleontology and Stratigraphy (RCPS), Jilin University. The fossil specimens and cuticle preparations are stored in the RCPS, in Changchun of China.

2.3. Stomatal analysis

The SI is calculated as: $SI(\%) = [SD/(SD + ED)] * 100$, where a SD = stomatal density, and ED = non-stomatal epidermal cell density (subsidiary cells and ordinary epidermal cells). The

Campanian atmospheric CO₂ levels are reconstructed from fossil *Ginkgo* cuticle SIs by using the inverse regression function (RF) (Royer et al., 2001b) given by:

$$\text{paleo} - \text{CO}_2 = \frac{(415 \times \text{SI} - 1961) \times 2000}{3337 \times \text{SI} - 2000} \quad (1)$$

Eq. (1) was derived from experiments of extant *Ginkgo biloba* L. leaves collected during the anthropogenic CO₂ increases of the past 200 years and greenhouse CO₂ enrichment. This function can be used for the Campanian material (*G. adiantoides*) owing to the extreme similarity in both ecological and anatomical features of these two forms (Tralau, 1968; Crane et al., 1990; Royer et al., 2003). In addition, the sedimentological and floral data from the quantitative survey of Royer et al. (2003) on 51 *Ginkgo*-bearing fossil sites indicate that *Ginkgo* was largely confined to disturbed stream margin and levee environments. These highly disturbed environments usually support well-watered, open-canopy forests that should lack intracanalopy CO₂ gradients (Royer, 2003).

To assess the results of this procedure, an alternative stomatal-based CO₂ method, nearest living equivalent (NLE) (McElwain and Chaloner, 1996; McElwain, 1998), was used, assuming a pre-industrial CO₂ concentration of 300 ppm.

3. Results

Estimated CO₂ concentrations from our stomatal index analyses vary from 558.83 ppm to 692.80 ppm for the full span of the Campanian using the RF methodology (Table 1). Overall, the records suggest a modest long-term decrease in pCO₂ with a background of ~550–590 ppm (Table 1; Fig. 3). However, a CO₂ spike, up to 692.80 ppm, is notable in the late Campanian on the basis of bed 6 (Fig. 3). This short-term CO₂ peak value is followed by a rapid return to background values of 592.02 ppm in bed 7 (Fig. 3). For the sake of simplicity in the following discussion, we refer to this type of paleo-CO₂ rise-fall as a short-term carbon dioxide fluctuation (SCDF). Similar SCDFs have been mostly recognized in the critical vegetation turnover intervals regardless of the magnitude, such as the T-J (McElwain et al., 1999), K-T (Beerling et al., 2002), Pal.-Eoc. (Royer et al., 2001b), and early-middle Miocene (Kürschner et al., 2008). All these botanical data suggest short-term couplings between atmospheric CO₂ and coeval geological events.

Table 1
Stomatal measurement and inferred paleo-CO₂ based on *G. adiantoides* from Taipinglinchang Formation

Bed	No. of leaves	SI (mean)	Standard deviation of SI	paleo-CO ₂ (RF)	RCO ₂	NLE			
						CO ₂ (Recent standard)	Sigma-1	CO ₂ (Carboniferous standard)	Sigma +1
11	10	7.01	0.14	558.53	1.62	484.78	436.30	969.55	1066.51
10	12	6.98	0.27	569.43	1.62	487.18	438.46	974.36	1071.79
9	7	6.97	0.43	571.03	1.63	487.52	438.77	975.04	1072.54
8	8	6.92	0.34	588.02	1.64	490.97	441.87	981.94	1080.14
7	11	6.91	0.27	592.02	1.64	491.74	442.57	983.48	1081.83
6	8	6.70	0.23	692.80	1.69	507.04	456.33	1014.07	1115.48
5	3	6.96	0.49	575.98	1.63	488.56	439.70	977.11	1074.83
4	5	6.98	0.31	567.38	1.62	486.74	438.06	973.48	1070.82
3	7	6.94	0.31	583.55	1.63	490.09	441.08	980.18	1078.20
2	5	6.93	0.50	584.90	1.63	490.36	441.32	980.72	1078.79
1	1	6.83	0.49	624.74	1.66	497.49	447.75	994.99	1094.49

In northeast China and the Russian Far East, there was a warming of climate from Santonian to Campanian indicated by the paleobotanical data (Herman, 1993; Sun et al., 2007b). The SCDF derived from *Ginkgo* cuticles of the Taipinglinchang Formation would be an additional evidence for paleoclimatic warming in the late Campanian.

4. Comparisons

To cross-test the Campanian CO₂ reconstructions, the new results are compared to estimates from geochemical proxies and

predictions from geochemical models of the long-term global carbon cycle. Additionally, a few paleobotanical data of Campanian CO₂ have been published to date, so that the comparisons are extended to stratigraphically adjacent stages, such as to the Early Cretaceous and to the Maastrichtian.

The present data of Campanian CO₂ concentration are most similar to the levels estimated by GEOCARB II of Berner (1994), but with slightly higher values (30 ppm on average). GEOCARB III (Berner and Kothavala, 2001) estimated higher pCO₂ values, but both RF- and NLE-based estimates match the error range (Fig. 4). Moreover, the present values lie between the GEOCARB II and III except for the Recent Standardization of NLE. Some authors (e.g. Haworth et al., 2005) have argued that the GEOCARB II model might be a more accurate reconstruction of pCO₂ for the mid-Mesozoic than GEOCARB III. It appears that this may also be the case for the Late Cretaceous.

The present paleo-CO₂ estimates are also similar to Wallmann (2001) except that the latter demonstrates a slight more rapid decline. The results from box model of Hansen and Wallmann (2003) illustrates a relative higher CO₂ concentration in the Campanian, but it is in the error range of the present study by

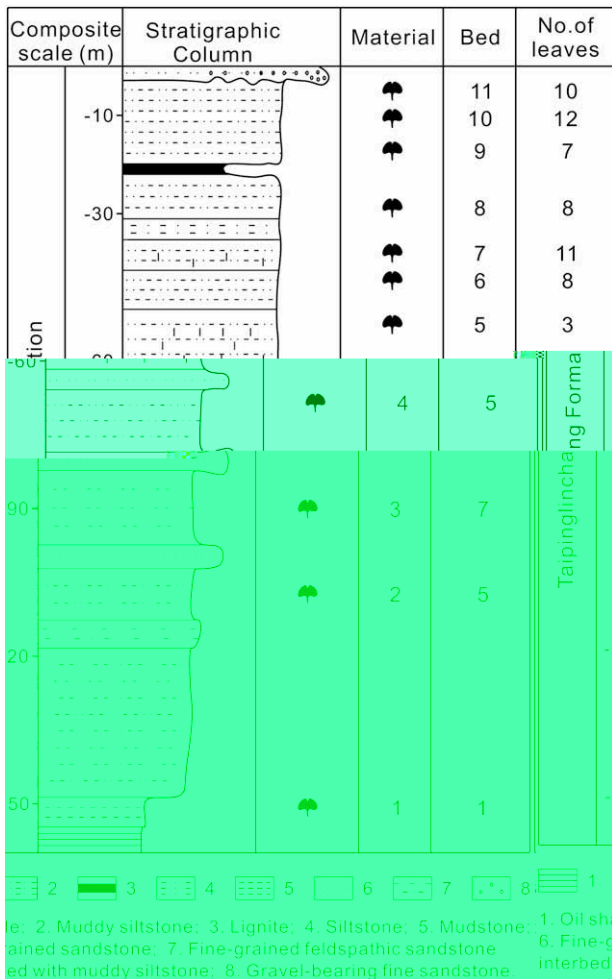


Fig. 2. Graphic log showing stratigraphic column (*Ginkgo* material sampled from 11 beds).

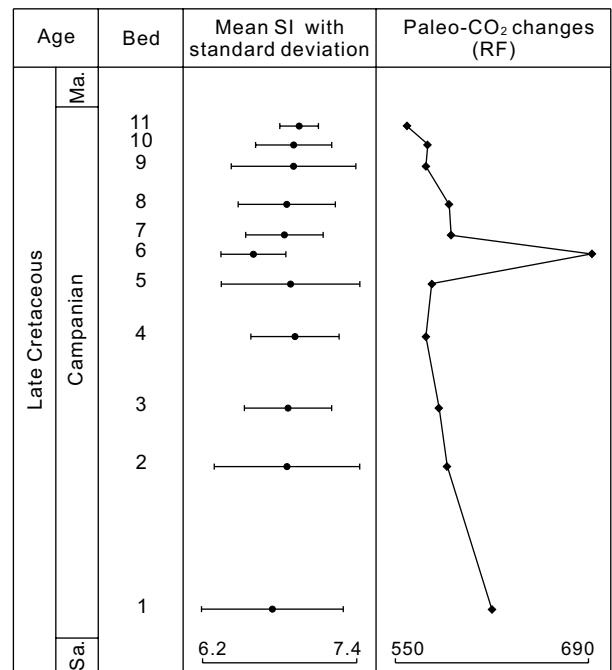


Fig. 3. pCO₂ estimates of the Campanian based on *G. adiantoides* from the Taipinglinchang Formation (stratigraphic framework after Sun et al., 2007b; error bars show standard deviation).

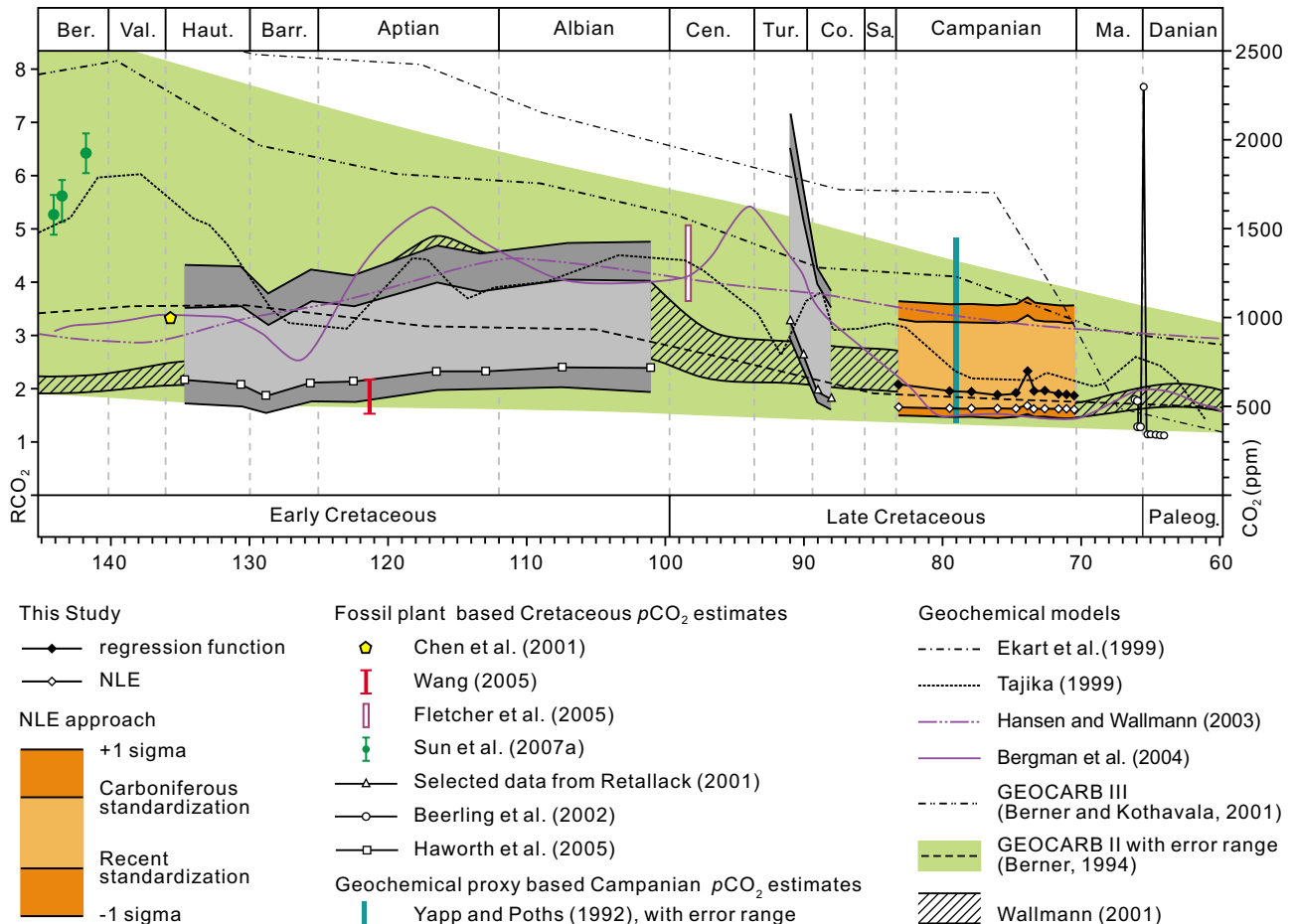


Fig. 4. Estimates of Cretaceous paleo- CO_2 from this study, previous data of geochemical models, geochemical and paleobotanical proxies.

NLE-based estimates (Fig. 4). Moreover, the minimum $p\text{CO}_2$ estimates by NLE of the present data strongly match those from the COPSE biogeochemical cycling model of Bergman et al. (2004) with the exception of the earliest Campanian (Fig. 4).

Ekart et al. (1999) obtained a Campanian CO_2 value of 1250 (± 500) ppm, and Yapp and Poths (1992) calculated a Campanian value of 1400 ppm, with an error range of greater than 1000 ppm. Thus, the present estimate is within the ranges proposed by previously published geochemical values albeit that the latter have large error bars.

Significantly, the late Campanian SCDF has not been recognized in the geochemical proxy (Ekart et al., 1999) or most geochemical models (Bernier, 1994; Bernier and Kothavala, 2001; Wallmann, 2001; Hansen and Wallmann, 2003; Bergman et al., 2004). This is likely due to the lower resolution of the geochemical approaches for the Cretaceous (ca. 10 Ma.). In Tajika's (1999) geochemical model, however, a slight SCDF has been recognized in the late Campanian at a resolution of ca. 10 Ma, which occurred just after the one identified from the new data (Fig. 4). These may relate to the same late Campanian SCDF, their positions differing only due to the quality of the stratigraphic resolution.

For botanical comparison, the NLE-based Campanian ratio of CO_2 (RCO_2) values of present study are calculated (Table 1; Fig. 4). The NLE of fossil *Ginkgo adiantoides* is obviously *G. biloba*, which yields 11.33 SI on average (Beerling and Royer, 2002b). The NLE-based values are calibrated with 300 ppm of recent standardization or 600 ppm of Carboniferous standardization, which are regarded as the broad minimum and maximum estimates of paleo- $p\text{CO}_2$ (McElwain, 1998).

Two studies have been undertaken based on *G. coriacea* Florin from the early-middle Early Cretaceous Huolinhe Formation in northeastern China. Chen et al. (2001) reported a RCO_2 of 2.8 whereas Sun et al. (2007a) inferred a RCO_2 of 2.55–3.20. Since no detailed sampling horizon information was provided by Chen et al. (2001), we presume the different results between these two studies reflect their different sampling horizons based on their respective stratigraphic illustrations.

Haworth et al. (2005) reported stomata-based values for mid-Cretaceous $p\text{CO}_2$ by using NLE. Their results show relatively low and only slight varying $p\text{CO}_2$ over the Hauterivian-Albian interval. Wang (2005) calculated the Early Cretaceous paleo- CO_2 at 1.55–2.18 RCO_2 , using NLE based on *G. coriacea*, *G. truncata* (Li) Chen, *G. sibirica* Heer and *G. adiantoides* from the Changcai Formation in Northeast China (Aptian age, Sun et al., 2005). His result is more similar to those of Haworth et al. (2005).

Retallack (2001) published fossil cuticle-based $p\text{CO}_2$ back to 300 Ma. However, some of the data suffer a large variability of SI because of the small sample size (commonly <4 cuticle fragments) and by the use of an inappropriate transfer function (Beerling and Royer, 2002b). We re-calculated the original ginkgoalean data near the Campanian from Retallack (2001) using the NLE rather than RF, because 1) the stomatal responses to CO_2 are species-specific (Royer, 2001); and 2) the original Turonian-Coniacian materials of Retallack (2001) are *Ginkgo pilifera* Samylnina and *G. transsenonicus* Krassilov, which commonly yield amphistomatic cuticles (Samylnina, 1967; Krassilov, 1979). The re-calibration demonstrates a dramatic reduction, from ~ 970 ppm to ~ 520 ppm, during the late Turonian-middle Coniacian at a resolution of ca. 1 million years

(Fig. 4). However, this $p\text{CO}_2$ reduction is not recognized in most geochemical models except that of Bergman et al. (2004). More detailed paleobotanical data are needed to confirm this SCDF due to the sparse materials used for its basis.

From the Albian to the earliest Campanian, the $p\text{CO}_2$ estimates show a gradual decrease from ~ 523 ppm to 497 ppm (NLE-based). This decrease trend is also supported by the geochemical data (e.g. Hansen and Wallmann, 2003; Fletcher et al., 2005) (Fig. 4). But they cannot exclude the possibility that additional SCDFs occurred during the Cenomanian-Santonian, as there is a lack of high-resolution data during this geological interval. After the late Campanian SCDF, it appears that no striking changes in paleo- $p\text{CO}_2$ occurred during the Maastrichtian, and levels gradually decreased to 530 ppm until the K-T event (Beerling et al., 2002; Beerling and Royer, 2002a; Royer et al., 2007).

5. Conclusions

Stomatal indices of *G. adiantoides* produce a $p\text{CO}_2$ background of 550–590 ppm. The overall trend of $p\text{CO}_2$ shows a gradual decrease through the Campanian, which is also shown by independent geochemical methods. Our SI-based $p\text{CO}_2$ estimate is more comparable to the GEOCARB II model. However, a short-term carbon dioxide fluctuation (SCDF) is recognized in the late Campanian (up to ~ 690 ppm), and represents a brief excursion from the trend of decreasing CO_2 through the Campanian. This SCDF is followed by a rapid return to background values of ~ 590 ppm.

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