Invited Review

Classification and systematics of the Fagopyrum species

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Fagopyrum (Polygonaceae) is a small genus including less than 30 species, mostly endemic to southern China. The genus includes two cultivated species, common buckwheat *F. esculentum* and Tartary buckwheat *F. tataricum. Fagopyrum* is clearly distinguished from other genus in Polygonaceae by the central position of embryo in achene. The genus is divided into two major groups, namely the cymosum group and the urophyllum group, based on morphological characters and molecular systematics. In the last three decades the number of species in the genus has doubled by the discovery of new species by Japanese and Chinese groups. Most of them are revealed to be included in the urophyllum group based on morphological and molecular genetic analyses. Molecular systematic surveys have also detected inappropriate treatment of some non-*Fagopyrum* species as new species or combination in the genus.

Key Words: classification, delineation of *Fagopyrum*, intraspecific variation, molecular systematics, new species.

Overview of the genus *Fagopyrum*, a group of cultivated and wild buckwheat species

Fagopyrum (Polygonaceae) is a small genus comprised of less than 30 species (Jin et al. 2018). Most of the wild species show narrow distribution areas in Southern Asia, mainly on the southeastern edge of Qinghai-Tibetan Plateau (Ohnishi 1998a). Two species, common buckwheat F. esculentum and Tartary buckwheat F. tataricum, are cultivated, and a wild species F. cymosum is utilized as forage and a source of pharmaceutical drugs (Wang et al. 2005). For common buckwheat and Tartary buckwheat, cultivated and wild forms are distinguished and classified as subspecies (Ohnishi 1998b). Wild common buckwheat F. esculentum ssp. ancestrale was discovered at the first time in 1990 (Ohnishi 1990, 1998a) at Yongsheng, Yunnan, China. Now wild common buckwheat is found in northwestern Yunnan, western Sichuan, and eastern Tibet around the Three Parallel Rivers region where the Jinsha or upper Yangtze, Mekong, and Salween rivers flowing down north to south in parallel (Ohnishi and Konishi 2001). F. esculentum ssp. ancestrale is thought of as wild ancestor of cultivated buckwheat F. esculentum ssp. esculentum (Ohnishi 1998a, 1998b). AFLP analysis revealed that wild common buckwheat populations distributed in eastern Tibet is the most closely related to cultivated forms (Konishi *et al.* 2005), indicating that cultivated common buckwheat was domesticated in the eastern Tibet to western Sichuan. Tsuji and Ohnishi (2000, 2001) performed phylogenetic analyses of cultivated (*F. tataricum* ssp. *tataricum*) and wild (*F. tataricum* ssp. *Potanini*) forms of Tartary buckwheat based on RAPD and AFLP data and showed that cultivated Tartary buckwheat was domesticated in eastern Tibet to northwestern Yunnan, the same area as the birthplace of common buckwheat.

The delineation of *Fagopyrum* differs among classification systems of Polygonaceae. Species recognized as the member of the genus *Fagopyrum* in the present day are listed in **Table 1**. Gross (1913) proposed many new combinations for the species in the section Polygoneae. In the study, two genera, *Tiniaria* and *Fagopyrum*, were reduced into a single genus *Fagopyrum* with respective sections Tiniaria and Eufagopyrum in the genus. Samuelsson (1929) listed 10 species in the section Fagopyrum of the genus *Polygonum*. Steward (1930) mostly followed the system of Samuelsson (1929) and included 10 species in the section Fagopyrum of the genus *Polygonum*. In the present day, most studies seem to follow the system of Hedberg (1946) that treats *Fagopyrum* as an independent genus.

Fagopyrum has been discriminated from other genera or sections by embryo morphology. Dammer (1894) stated a key to *Fagopyrum* as large folded cotyledons in achene. Gross (1913) characterized the section Eufagopyrum by

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Table 1. Fagopyrum species

Group	Species	Distribution of natural populations	Chromosome number	Mating system	Reference
cymosum	F. esculentum	Sichuan, Yunnan, Tibet	16	SI	Moench (1794), Ohnishi (1998a)
	F. homotropicum	Sichuan, Yunnan, Tibet	16, 32	SC	Ohnishi (1998a)
	F. tataricum	Sichuan, Yunnan, Tibet, Nepal, Pakistan	16	SC	Gaertner (1791)
	F. cymosum	Southern China, Nepal, India, Bhutan, Myanmar, Vietnam, Thailand	16, 32	SI	Meisner (1857)
urophyllum	F. urophyllum	Sichuan, Yunnan	16	SI	Gross (1913)
	F. lineare	Yunnan	16	SI	Haraldson (1978)
	F. leptopodum	Sichuan, Yunnan	16	SI	Hedberg (1946)
	F. statice	Yunnan	16	SI	Gross (1913)
	F. gracilipes	Sichuan, Yunnan, Bhutan	32	SC	Diels (1901)
	F. capillatum	Yunnan	16	SI	Ohnishi (1998a)
	F. rubifolium	Sichuan	32	SC	Ohsako and Ohnishi (1998)
	F. gracilipedoides	Yunnan	16	SI	Ohsako et al. (2002)
	F. gilesii	Yunnan	16	SI	Hedberg (1946)
	F. jinshaense	Yunnan	16	SI	Ohsako et al. (2002)
	F. pleioramosum	Sichuan	16	SC	Ohnishi (1998a)
	F. callianthum	Sichuan	16	SC	Ohnishi (1998a)
	F. macrocarpum	Sichuan	16	SC	Ohsako and Ohnishi (1998)
	F. tibeticum	Tibet	48	unknown	Tian et al. (2011)
	F. pugense	Sichuan	16	SC	Tang et al. (2010)
	F. qiangcai	Sichuan	16	SC	Shao et al. (2011)
	F. luojishanense	Sichuan	16	SC	Hou et al. (2015)
	F. crispatifolium	Sichuan	32	SC	Liu et al. (2008a)
	F. longzhoushanense	Sichuan	16	SC	Wang et al. (2017)
	F. densovillosum	Sichuan	16	SC	Liu et al. (2008b)
Ambiguous	F. wenchuanense	Sichuan	16	SC	Shao et al. (2011)

conduplicate cotyledons or embryo in the central region in achene. Nakai (1926) also distinguished Fagopyrum by the centered position of embryo with conduplicate cotyledons. Two subgroups have often been recognized within Fagopyrum. Gross (1913) discriminated two subgroups in the section Eufagopyrum based on morphology of inflorescence and perianth on achene. The subgroups composed of F. esculentum, F. tataricum, F. cymosum, F. suffruticosum and F. odontopterum (F. gracilipes var. odontopterum) was characterized by cymose inflorescence with many branching and dense flowers and the other subgroups including F. maireii (F. urophyllum), F. bonatii (F. gracilipes), F. Grossii (F. leptopodum var. Grossii), F. statice and F. tristachyum (F. cymosum) by racemose inflorescence with sparse flowers. Roberty and Vautier (1964) amalgamated Fagopyrum species into two species based on the achene size. They united F. esculentum, F. cymosum, and F. tataricum into F. esculentum sensu lato and F. gilesii, F. Grossii, F. gracilipes, F. statice and F. urophyllum into F. gilesii sensu lato. These groupings are mostly concordant with the cymosum group and the urophyllum group of Yasui and Ohnishi (1998a). Differentiation between the cymosum and the urophyllum groups is strongly supported by both morphological characters and molecular data (described in detail below). Ohnishi and Matsuoka (1996) defined two characters discriminating the two groups: laterally long cotyledons and achene partially covered with perianths as the key character of the cymosum group and round to longitudinally long cotyledons and achene completely covered with perianths as the key character of the urophyllum group (**Fig. 1**).

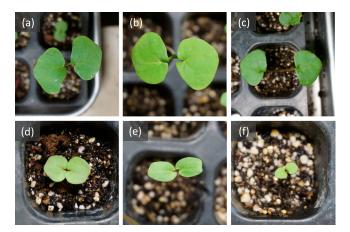


Fig. 1. Cotyledons of *Fagopyrum* species. (a) *F. esculentum* ssp. *esculentum*, (b) *F. tataricum* ssp. *tataricum*, (c) *F. cymosum*, (d) *F. urophyllum*, (e) *F. callianthum*, and (f) *F. leptopodum*.

Diversity of mating system in the genus

About half of the *Fagopyrum* species exhibit heterostyly with short style-high anther flowers (thrum) and long stylelow anther flowers (pin). Most species showing heterostyly also have self-incompatibility (SI), but some species such as *F. pleioramosum*, *F. callianthum*, and *F. macrocarpum* are self-compatible. Other species have homostylous selfcompatibility (SC). Mating system of the two cultivated species is contrasting; common buckwheat exhibits heterostylous SI whereas Tartary buckwheat homostylous SC. In contrast to SI with homomorphic flowers in other families such as Brassicaceae and Solanaceae, the degree of SI of common buckwheat is extremely high such that self-fertilization rarely occurs. The possibility of selfing is slightly higher in thrum plants than in pin plants (Garber 1927).

Chromosome number

Basic chromosome number of *Fagopyrum* species has been known to be x = 8. Most species are diploid with 2n = 16. *F. gracilipes* and *F. rubifolium* are tetraploid with 2n = 32. *F. cymosum* and *F. homotropicum* have both diploid and tetraploid forms (Ohnishi and Asano 1999). *F. tibeticum* has a unique karyotype with a chromosome number 2n = 48 (Tian *et al.* 2009).

Recent discovery of the new species of *Fagopyrum* and their systematic position in the genus

Haraldson (1978) listed 12 species including a new combination F. lineare, which was originally described as a member of Polygonum section Fagopyrum by Samuelsson (1929). Samuelsson described two new species, P. lineare and P. caudatum in the section Fagopyrum of the genus Polygonum. In 1990s, Ohnishi and colleagues discovered a total of eight new species and one new subspecies (Ohnishi 1998a, Ohsako and Ohnishi 1998, Ohsako et al. 2002). Discovery of wild common buckwheat F. esculentum ssp. ancestrale (Ohnishi 1990) contributed largely to clarify the origin and domestication of common buckwheat. Intensive survey of wild common buckwheat revealed that the subspecies is distributed around the Three Parallel Rivers region from Tibet-Sichuan border to northwestern Yunnan (Ohnishi and Konishi 2001). The other important species is F. homotropicum. This species is morphologically very similar to wild common buckwheat but differs in that the species exhibits homostylous SC (Ohnishi 1998a). Distribution area of F. homotropicum is like that of wild common buckwheat but F. homotropicum shows wider distribution (Ohsako et al. 2017, Tomiyoshi et al. 2012). Other new species F. capillatum, F. pleioramosum, F. callianthum, F. rubifolium, F. macrocarpum, F. jinshaense, and F. gracilipedoides share key characters of the urophyllum group (Ohnishi 1998a, Ohsako and Ohnishi 1998, Ohsako 2002). F. capillatum, F. rubifolium and et al. F. gracilipedoides are morphologically similar to F. gracilipes. These four species have heavily pubescent stipule and leaf blade (Ohsako and Ohnishi 1998, Ohsako et al. 2002). F. capillatum and F. gracilipedoides are diploid with chromosome number 2n = 16 and possess heterostylous SI. F. rubifolium is a self-compatible tetraploid (Ohsako and Ohnishi 1998). F. pleioramosum, F. callianthum, and F. macrocarpum have relatively large flower and achene in the urophyllum group. Especially, flowers and achenes of F. callianthum and F. macrocarpum are the largest within the group (Ohsako and Ohnishi 1998). In addition, they share heterostylous SC. This characteristic is unique to these species in the genus (Ohsako and Ohnishi 1998). They are endemic to upper Min river valley in Sichuan (Ohnishi 1998a, Ohsako and Ohnishi 1998). F. jinshaense is endemic to Jinsha river valley of northwestern region of Yunnan. This species has similar morphological characters to F. gilesii but differs in morphology of inflorescence. F. gilesii has compact inflorescences with quietly short internodes whereas internodes on inflorescence of F. jinshaense elongate as seen in the other species in the urophyllum group (Ohsako et al. 2002).

Phylogenetic studies of Fagopyrum had not been conducted until application of molecular genetic techniques to phylogenetic analysis become widespread in plant systematics. Ohnishi and Matsuoka (1996) applied isozyme markers and RFLP of chloroplast DNA (cpDNA) to phylogenetic inference of the genus Fagopyrum. Both data sets clarified that the genus is divided into two major groups, one including two cultivated species F. esculentum and F. tataricum and their wild relative F. cymosum and the other composed of other wild species with small achene. Yasui and Ohnishi (1998a) investigated the phylogeny of Fagopyrum including a new species F. homotropicum using nucleotide sequences of *rbcL-accD* region of cpDNA. They also showed the two major groups in the genus, and they named these as the cymosum group and urophyllum group, respectively. They further surveyed nucleotide sequences of internal transcribed spacer (ITS) of nuclear ribosomal RNA gene (Yasui and Ohnishi 1998b) to confirm the results obtained from cpDNA data. Phylogenies based on these four data sets showed good concordance with each other. These analyses clarified that (1) in the cymosum group, F. tataricum and F. cymosum are monophyletic and F. homotropicum is sister to F. esculentum, and (2) in the urophyllum group, new species F. capillatum is sister to F. gracilipes and F. pleioramosum and F. callianthum form a monophyletic group. Ohsako and Ohnishi (1998, 2000) and Ohsako et al. (2002) investigated phylogenetic relationships among species in the urophyllum group including new species F. rubifolium, F. macrocarpum, F. gracilipedoides, and F. jinshaense using allozymes and nucleotide sequences of ITS and cpDNA regions. These studies clarified that (1) F. rubifolium and

F. gracilipedoides form a monophyletic group with morphologically similar species *F. gracilipes* and *F. capillatum*, (2) *F. macrocarpum* is sister to *F. pleioramosum*, and (3) *F. jinshaense* is distantly related to *F. leptopodum* and *F. gilesii* despite their morphological similarity. Recent phylogenetic study revealed that a woody plant *Parapteropyrum tibeticum* is a member of *Fagopyrum* (Sanchez *et al.* 2009, Tian *et al.* 2011). This species was included into *Fagopyrum* under a new combination *F. tibeticum* (Sanchez *et al.* 2011). Phylogenetic relationships among *Fagopyrum* species, including new species and combination, are summarized in **Fig. 2**.

The members of *Fagopyrum* have dramatically increased during the last two decades by the discovery of new species. Chen (1999) described three species, *F. zuogongense*, *F. megaspartanium*, and *F. pilus*. *F. zuogongense* was found in Zuogong county of southeastern part of Tibet. The species is morphologically similar to *F. esculentum* but differs in that it is self-compatible and tetraploid. This plant is thought to be a type of tetraploid form of *F. homotropicum* based on its geographical distribution and characteristics in morphology, ecology, and chromosome number (Tsuji *et al.* 1999). *F. megaspartanium* and *F. pilus* are also indistinguishable from *F. cymosum* in morphology and should be treated as variation of *F. cymosum* (Tsuji *et al.* 1999).

Recently Zhou and colleagues reported several new species, most of which possibly belong to the urophyllum group. *F. pugense* (Tang *et al.* 2010) was first found in Luojishan, Puge county, Sichuan. This species is reported to show similar morphology to *F. gracilipes* whereas the chromosome number is 2n = 16. Photograph in Zhou and

Ohnishi (2018) show shared characters between the species such as dense pubescence on stem and ochrea, small homostylous flower with slightly pink-colored perianths, and dentate wings on the edges of achene. The illustration presented in the original report indicates that the species bears heterostylous flowers as F. capillatum, a sister species of F. gracilipes (Yasui and Ohnishi 1998a, 1998b). However, F. pugense and F. capillatum should be treated as different species because F. pugense is partially self-fertilizing whereas F. capillatum is self-incompatible. Zhou and Ohnishi (2018) reported that F. pugense is also seen in Yanyuan, Huili, Huidong, Butuo, Zhaojue, Meigu, Mianning, Luding, and Kangding counties. Ohnishi explored some of these locations and did not find new species corresponding to F. pugense whereas he detected and collected F. gracilipes accessions in Yanyuan, Mianning, Kangding, and Luding. F. densovillosum (Liu et al. 2008b), F. luojishanense (Hou et al. 2015), and F. longzhoushanense (Wang et al. 2017) were also reported as diploid close relative of F. gracilipes. All these new species were discovered in Puge, Sichuan. They show similarity in karyotypes defined by chromosome number and arm ratios. They are discriminated merely by some quantitative traits such as stem thickness and morphology of wings on edges of achene. Molecular systematic survey considering intraspecific variation might contribute to reduce some of these species into a single species by treating them as different subspecies or varieties. Cross experiments might also be useful to confirm the validity of the classification because reproductive isolation could serve as a criterion for species delineation in the genus (Ohsako et al. 2002).

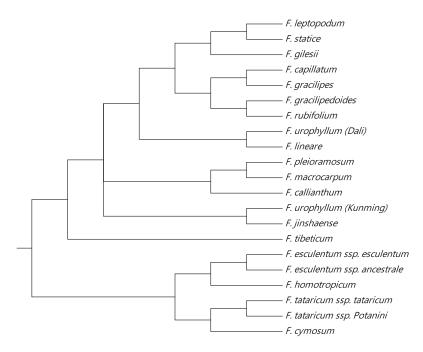


Fig. 2. Phylogenetic relationships among *Fagopyrum* species by building a consensus of the previous results of molecular systematic studies. Species without clear phylogenetic positions are not included.

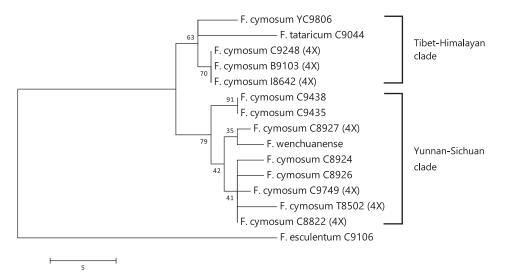


Fig. 3. Phylogenetic relationships among diploid and tetraploid accessions of *F. cymosum*, *F. tataricum*, and *F. wenchuanense* inferred by parsimony method based on nucleotide sequences of *matK* region of cpDNA (GenBank accession AB093071–AB093087 and JF829982).

Liu *et al.* (2008a) described another new species *F. crispatifolium* as a close relative to *F. gracilipes*. This species is self-fertilizing tetraploid with a chromosome number 2n = 32. The unique characteristic of *F. crispatifolium* is rugged texture of leaf surface. Molecular systematic studies showed that the species is closely related to *F. gracilipes* and *F. pugense* (Jin *et al.* 2018, Zhou *et al.* 2012).

F. qiangcai was found at Kaku village, Wenchuan, where F. pleioramosum and F. callianthum distribute (Shao et al. 2011). F. qiangcai bears heterostylous flowers with pink perianths and sagittate leaves with red veins. These characteristics are very similar to those of F. callianthum (Ohnishi 1998a). These circumstances lead to the expectation that F. qiangcai is a very close relative or conspecific variation of F. callianthum, whereas comparative study has not yet been conducted. F. wenchuanense was reported as a new species from Wenchuan, Sichuan (Shao et al. 2011). This species has a chromosome number 2n = 16. The authors claim that the species is morphologically similar to F. gracilipes, but it seems to be closely related to F. pleioramosum based on chromosome number and morphological characters such as prostrate branch and hastate to cordate leaf slightly pubescent on both sides. These characteristics are well represented on the illustration in the paper and the photograph in a recently published book (Ohnishi and Zhou 2018). In addition, the illustration of F. wenchuanense in Shao et al. (2011) includes figures of short-styled and long-styled flowers, strongly suggesting that the species is heterostylous like F. pleioramosum. Surprisingly, F. wenchuanense was shown to be included in the cymosum group and closely related to F. cymosum by molecular systematic study (Zhou et al. 2014). The molecular data of F. wenchuanense can be analyzed in the context of the intraspecific diversity of F. cymosum because comparable sequences are available for multiple accessions of *F. cymosum* (Yamane *et al.* 2003). Phylogenetic analysis of the cymosum group based on *matK* sequences indicated that the nucleotide sequence of *F. wenchuanense* is included in the Yunnan-Sichuan clade of *F. cymosum* (**Fig. 3**). If this phylogeny precisely reflects the evolutionary relationships among species, *F. wenchuanense* was derived from *F. cymosum* in Yunnan to Sichuan and acquired many morphological characteristics common to the species of urophyllum group by parallel evolution. These evolutionary events seem quite unlikely to occur. Molecular systematic studies using multiple accessions of the species and different markers on nuclear genome is needed to clarify evolutionary position of the species.

Differentiation within species

Plant species usually exhibit considerable level of intraspecific variation both at phenotypic and molecular levels. When reconstructing phylogenetic relationships among closely related species, effects of intraspecific variation on the phylogenetic inference should be considered. Some studies on intraspecific differentiation within Fagopyrum species have shown that different lineages often exhibit nonmonophyly in relation to their sister species. A highly variable species F. leptopodum is sister to F. statice at species level, but lineages of these species intermingled with each other in the phylogeny based on nucleotide sequences of cpDNA regions (Ohsako and Ohnishi 2000, 2001). The phylogenetic relationships among accessions suggest that two groups of F. statice derived independently from different ancestral lineages of F. leptopodum or northern lineage of F. statice has hybrid origin between F. leptopodum and southern lineage of F. statice. Systematic studies have shown that a perennial species F. urophyllum is comprised of two subgroups highly differentiated from each other (Ohsako and Ohnishi 2000, Yasui and Ohnishi 1998a,

1998b). Kawasaki and Ohnishi (2006) investigated cpDNA variation within F. urophyllum using a total of 19 accessions covering the entire distribution range of the species. They confirmed that the accessions are separated into two phylogeographic groups, the Kunming and the Dali groups. These groups are distributed around central area of Yunnan and northwestern Yunnan-southern Sichuan region, respectively. They were positioned distantly to each other in the reconstructed phylogeny. The Kunming group became sister to F. jinshaense and the Dali group to F. lineare. This phylogenetic pattern suggests that these groups should be recognized as distinct species. Further investigation on morphological characters, ploidy level, reproductive isolation, and genomic variation is needed to refine taxonomic treatment of the species. Another perennial buckwheat species F. cymosum has also been known to be highly polymorphic both at morphological and molecular levels (Yasui and Ohnishi 1998a, 1998b). Molecular systematic analyses revealed that F. cymosum is more closely related to F. tataricum than to F. esculentum (Ohnishi and Matsuoka 1996, Yasui and Ohnishi 1998a, 1998b). Yamane et al. (2003) investigated intra- and interspecific relationships between F. cymosum and F. tataricum and revealed that (1) F. cymosum is divided into two groups that are geographically isolated by Hengduan Mountains, namely Yunnan-Sichuan clade and Tibet-Himalayan clade, (2) both groups were comprised of diploid and tetraploid forms, and (3) F. tataricum is included in Tibet-Himalayan clade.

Delineation of the genus by molecular systematic study

Molecular data, especially nucleotide sequences of nuclear and organellar genome regions, have provide powerful means to delineate the genus Fagopyrum and validate the description new species and combinations. of F. megacarpum was originally described by Hara (1972). Afterward Hara (1982) placed the species in the genus Eskemukerjea under a new combination E. megacarpum. However, the species was placed again in *Fagopyrum* by Hong (1988) based on pollen morphology. F. megacarpum is endemic to Nepal, geographically apart from the species diversity center of Fagopyrum. Ohsako et al. (2001) surveyed phylogenetic position of F. megacarpum using nucleotide sequence of the *rbcL-accD* region of cpDNA. The rbcL phylogeny including two Persicaria and one Rumex species showed that F. megacarpum became sister to R. acetosella and excluded from monophyletic group comprised of all other species of Fagopyrum. Based on this result, F. megacarpum should not be treated as a member of Fagopyrum. Zhou et al. (2015) reported a new species F. hailuogouense from Luding, Sichuan. This plant is perennial forming rhizomes. Jin et al. (2018) surveyed illustration and photographs in the thesis by Zhang (2013) and Zheng (2012) and found that the F. hailuogouense is a synonym of Bistorta pergracilis. They also showed that the plant occupied a position far from *Fagopyrum* and lied in the genus *Bistorta* in phylogenetic tree using a nucleotide sequences of a diverse array of species in Polygonoideae. Phylogenetic analysis by Jin *et al.* (2018) also confirmed that *Pterxygonum giraldii*, often treated as a member of *Fagopyrum*, is not a member of *Fagopyrum* but is a sister to *Pteroxygonum denticulatum*. Molecular phylogeny is a powerful tool to support classification of species and higher taxa, but comprehensive sampling is important to obtain precise conclusion on the systematic and taxonomic issues, as claimed by Jin *et al.* (2018).

Author Contribution Statement

TO conducted phylogenetic analysis. TO and CL wrote the paper.

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