

Getting a hold on archaeal type IV pili: an expanding repertoire of cellular appendages implicates complex regulation and diverse functions

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A commentary on

Novel pili-like surface structures of *Halobacterium salinarum* strain R1 are crucial for surface adhesion

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Type IV pili (T4P) are a group of cell surface appendages of particular interest due to broad conservation and functional versatility across the domains *Bacteria* and *Archaea* (Albers and Meyer, 2011; Giltner et al., 2012). All T4P are composed of small protein subunits known as pilins that polymerize into helical fibers through the action of assembly ATPases (Giltner et al., 2012). This core ancestral machinery has been adapted in various lineages for many cellular processes—from adhesion and biofilm formation, to motility, horizontal gene transfer (HGT) and even electricity conduction (Giltner et al., 2012; Berry and Pelicic, 2015). When T4P structures are involved in adhesion, they are known as pili, if they no longer mediate attachment, but are associated with another function, such as scavenging macromolecules (e.g., DNA uptake by Com proteins in *Bacillus subtilis*), or secretion of proteins through a piston-like structure (i.e., type II secretion), they are called pseudopili (Averhoff and Friedrich, 2003; Peabody et al., 2003; Chen et al., 2005). T4P appendages may also contribute to both adhesion and another function. This dual function is sometimes true for archaea: a major group of archaeal T4P appendages characterized by the ability to rotate and enable swimming motility. Archaea are functionally analogous yet structurally and genetically unrelated to bacterial flagella (Jarrell and Albers, 2012; Shahapure et al., 2014; Albers and Jarrell, 2015). T4P have been studied to a greater extent in bacteria, in part because they are often virulence factors (Giltner et al., 2012). However, recent investigations have revealed a repertoire of archaeal T4P—highlighting implications for regulatory complexity and functional diversity.

Losensky et al. (2014) demonstrated that adhesive filaments in the haloarchaeon *Halobacterium salinarum* R1 observed during biofilm formation (Fröls et al., 2012) are dependent on the pilus assembly ATPase gene *pilB1* (Losensky et al., 2014), expanding the list of experimentally studied archaeal T4P (Table 1). Deletion of *pilB1* led to a lack of pili as observed through electron microscopy and a defect in adhesion. Only 4% of a glass surface was colonized by non-piliated/non-archaeallated cells ($\Delta flaI/\Delta pilB1$), relative to 36 and 44% for the parental and non-archaeallated ($\Delta flaI$) strains, respectively. The molecular composition of PilB1-dependent pili has not yet been determined, however Losensky and coauthors noted that there are over 30 candidate pilins in the *Hbt. salinarum* R1 genome, as indicated by the class III signal peptide prediction program FlaFind (Szabó et al., 2007b). FlaFind was used previously to show that most archaeal genomes

TABLE 1 | Experimentally studied type IV pili in archaeal species: archaella, adhesive pili, and pseudopili.^a

Structure name	Function/ associated phenotype	Characterized in (genera)	Filament diameter (nm)	References
ARCHAELLA				
	Swimming motility and involved in adhesion in some species; functionally analogous but evolutionarily and structurally distinct from the bacterial flagella ^b	<i>Halobacterium</i> <i>Haloferax</i> <i>Haloquadratum</i> <i>Sulfolobus</i> <i>Methanococcus</i> <i>Methanocaldococcus</i> <i>Pyrococcus</i>	10–15	Alam and Oesterhelt, 1984; Gerl and Sumper, 1988; Patenge et al., 2001; Streif et al., 2008 Tripepi et al., 2010, 2012, 2013 Alam et al., 1984 Szabó et al., 2007a; Lassak et al., 2012b; Shahapure et al., 2014 Bardy et al., 2002; Jarrell et al., 2011 Bellack et al., 2011 Nather et al., 2006; Nather-Schindler et al., 2014
ADHESIVE PILI				
Archaeal adhesive pilus (Aap)	Surface adhesion	<i>Sulfolobus</i>	11	Henche et al., 2012
Type IV pilus (Epd)	Surface adhesion	<i>Methanococcus</i>	8.5	Vandyke et al., 2008; Wang et al., 2008; Nair et al., 2013
Type IV pilus (PilA)	Surface adhesion	<i>Haloferax</i>	8–12	Esquivel et al., 2013; Esquivel and Pohlschröder, 2014, 2015
PilB1-dependent adhesive pilus-like ^c	Surface adhesion	<i>Halobacterium</i>	7–8	Losensky et al., 2014
UV-inducible pilus (Ups)	Autoaggregation and species specific DNA exchange following UV-irradiation	<i>Sulfolobus</i>	10	Fröls et al., 2008; Ajon et al., 2011
PSEUDOPILUS-LIKE				
Bindosome assembly system (Bas)	Sugar binding; also involved in cellular morphology and S-layer architecture	<i>Sulfolobus</i>	ND	Zolghadr et al., 2007, 2011

ND, not determined.

^aAs reviewed by Pohlschröder et al. (2011), Lassak et al. (2012a), Jarrell et al. (2013) and Esquivel and Pohlschröder (2015).

^bSee Jarrell and Albers (2012), Shahapure et al. (2014) and Albers and Jarrell (2015) for a review of how the archaellum came to be recognized as a unique archaeal motility structure, including a more comprehensive categorization of characterized archaella.

^cThe appendages characterized by Losensky et al. (2014) are listed as pilus-like because they have yet to be purified and biochemically verified. They may in fact be composed of homologs of PilA pilin proteins in *H. volcanii*, which are found in many euryarchaeal species (Esquivel et al., 2013).

contain many pilin/archaeellin homologs (Szabó et al., 2007b; Esquivel et al., 2013). For example, *Haloarcula marismortui* and *Haloferax volcanii* have nearly 50 putative pilin/archaeellin precursors (Esquivel et al., 2013).

Some of these pilins could be associated with additional functions. *Hfx. volcanii* has an ability for social motility in static liquid (Chimileski et al., 2014) and T4P could be involved in this activity (Esquivel and Pohlschröder, 2015), whereby they may attach to extracellular matrix along the substratum, similar to the S-motility system that pulls *Myxococcus xanthus* cells forward (Hodgkin and Kaiser, 1979; Zusman et al., 2007). There could be more archaeal T4P-related surface structures that scavenge macromolecules as well, like the bindosome of *Sulfolobus solfataricus* (Zolghadr et al., 2007, 2011).

Investigations of archaeal T4P leave open the possibility for undiscovered mechanisms for contacting abiotic surfaces or other cells. For instance, even in the non-piliated/non-archaeallated *Hbt. salinarum* strain, adhesion was not completely abolished (Losensky et al., 2014). Similar residual adhesion has been observed in *Hfx. volcanii* (Tripepi et al., 2010, 2013). In both cases, pilins that remain present in the membrane but cannot be

assembled into pili without the assembly ATPase(s) likely explain low levels of adhesion (Esquivel and Pohlschröder, 2014). There are two other cell-to-cell contact phenomena in *Hfx. volcanii* that do not require archaella or pili: Ca²⁺ dependent autoaggregation (Tripepi et al., 2010), and an HGT mechanism known as mating (Rosenshine et al., 1989; Tripepi et al., 2010; Naor et al., 2012). Additional types of extracellular polymers or fibers found in bacterial species could be present in archaea, such as amyloid protein (Chimileski et al., 2014). Unusual, genetically ambiguous non-T4P structures have already been observed in other archaeal species, including the hamus of the SM1 euryarchaeon (Moissl et al., 2005; Perras et al., 2014) and the cannulae of *Pyrodictium* cells (Nickell et al., 2003).

A plausible explanation for having a wide array of appendages is a capacity for differential regulation (Jarrell, 2012; Lassak et al., 2012a; Jarrell et al., 2013). Indeed, a number of studies point to dynamic regulatory systems controlling archaeal T4P. In *Hbt. salinarum*, *pilB1* expression was upregulated relative to *flaI* in adherent cells (Losensky et al., 2014), suggesting archaella and pili have antagonistically regulated functions in motility (when a planktonic state is favorable) and for adhesion (during biofilm

formation), as in *Hfx. volcanii* (Tripepi et al., 2010; Esquivel and Pohlschröder, 2014, 2015). *Haloarcula marismortui* has two archaeallins that are expressed under different temperatures and salinities (Syutkin et al., 2014), termed ecoparalogs. Likewise, the six *Hfx. volcanii pilA* paralogs, any one of which can restore adhesion when expressed in a null mutant [$\Delta pilA(1-6)$] (Esquivel et al., 2013), may be ecoparalogs as well. Intriguingly, deleting *flgA2*, one of two archaeallin genes in *Hfx. volcanii*, produced a hypermotile phenotype, rather than a motility defect (Tripepi et al., 2013). Archaeallins are also regulated through N-glycosylation (Guan et al., 2012; Tripepi et al., 2012) and regulatory proteins controlling adhesive pili and archaeella have been identified in *Sulfolobus acidocaldarius* (Reimann et al., 2012; Orell et al., 2013; Vassart et al., 2013).

As more T4P are described in archaeal groups, a common theme is appearing. A multitude of individual pilins/archaeallins

from one or more loci may appear to be redundant—contributing to appendages that are difficult to differentiate through electron microscopy and often depend on the same assembly ATPase. However, to the contrary, the maintenance of more than one pilus and archaeallum subunit gene is likely due to a complex regulatory network and the corresponding advantages of functional versatility. Subsets of pilins may be expressed in different combinations as a response to a variety of specific environmental conditions and/or cellular functions.

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References

- Ajon, M., Fröls, S., Van Wolferen, M., Stoecker, K., Teichmann, D., Driessen, A. J., et al. (2011). UV-inducible DNA exchange in hyperthermophilic archaea mediated by type IV pili. *Mol. Microbiol.* 82, 807–817. doi: 10.1111/j.1365-2958.2011.07861.x
- Alam, M., Claviez, M., Oesterhelt, D., and Kessel, M. (1984). Flagella and motility behavior of square bacteria. *EMBO J.* 3, 2899–2903.
- Alam, M., and Oesterhelt, D. (1984). Morphology, function and isolation of halobacterial flagella. *J. Mol. Biol.* 176, 459–475.
- Albers, S.-V., and Jarrell, K. F. (2015). The archaeallum: how archaea swim. *Front. Microbiol.* 6:23. doi: 10.3389/fmicb.2015.00023
- Albers, S. V., and Meyer, B. H. (2011). The archaeal cell envelope. *Nat. Rev. Microbiol.* 9, 414–426. doi: 10.1038/nrmicro2576
- Averhoff, B., and Friedrich, A. (2003). Type IV pili-related natural transformation systems: DNA transport in mesophilic and thermophilic bacteria. *Arch. Microbiol.* 180, 385–393. doi: 10.1007/s00203-003-0616-6
- Bardy, S. L., Mori, T., Komoriya, K., Aizawa, S. I., and Jarrell, K. F. (2002). Identification and localization of flagellins FlaA and FlaB3 within flagella of *Methanococcus voltae*. *J. Bacteriol.* 184, 5223–5233. doi: 10.1128/jb.184.19.5223-5233.2002
- Bellack, A., Huber, H., Rachel, R., Wanner, G., and Wirth, R. (2011). *Methanocaldococcus villosus* sp. nov., a heavily flagellated archaeon that adheres to surfaces and forms cell-cell contacts. *Int. J. Syst. Evol. Microbiol.* 61, 1239–1245. doi: 10.1099/ijs.0.023663-0
- Berry, J. L., and Pelicic, V. (2015). Exceptionally widespread nanomachines composed of type IV pilins: the prokaryotic Swiss Army knives. *FEMS Microbiol. Rev.* 39, 1–21. doi: 10.1093/femsre/fuu001
- Chen, I., Christie, P. J., and Dubnau, D. (2005). The ins and outs of DNA transfer in bacteria. *Science* 310, 1456–1460. doi: 10.1126/science.1114021
- Chimileski, S., Franklin, M. J., and Papke, R. T. (2014). Biofilms formed by the archaeon *Haloferax volcanii* exhibit cellular differentiation and social motility, and facilitate horizontal gene transfer. *BMC Biol.* 12:65. doi: 10.1186/s12915-014-0065-5
- Esquivel, R. N., and Pohlschröder, M. (2014). A conserved type IV pilin signal peptide H-domain is critical for the post-translational regulation of flagella-dependent motility. *Mol. Microbiol.* 93, 494–504. doi: 10.1111/mmi.12673
- Esquivel, R. N., and Pohlschröder, M. (2015). Archaeal type IV pili and their involvement in biofilm formation. *Front. Microbiol.* 6:190. doi: 10.3389/fmicb.2015.00190
- Esquivel, R. N., Xu, R., and Pohlschröder, M. (2013). Novel archaeal adhesion pilins with a conserved N terminus. *J. Bacteriol.* 195, 3808–3818. doi: 10.1128/JB.00572-13
- Fröls, S., Ajon, M., Wagner, M., Teichmann, D., Zolghadr, B., Folea, M., et al. (2008). UV-inducible cellular aggregation of the hyperthermophilic archaeon *Sulfolobus solfataricus* is mediated by pili formation. *Mol. Microbiol.* 70, 938–952. doi: 10.1111/j.1365-2958.2008.06459.x
- Fröls, S., Dyall-Smith, M., and Pfeifer, F. (2012). Biofilm formation by haloarchaea. *Environ. Microbiol.* 14, 3159–3174. doi: 10.1111/j.1462-2920.2012.02895.x
- Gerl, L., and Sumper, M. (1988). Halobacterial flagellins are encoded by a multigene family. *J. Biol. Chem.* 263, 13246–13251.
- Giltner, C. L., Nguyen, Y., and Burrows, L. L. (2012). Type IV pilin proteins: versatile molecular modules. *Microbiol. Mol. Biol. Rev.* 76, 740–772. doi: 10.1128/MMBR.00035-12
- Guan, Z., Naparstek, S., Calo, D., and Eichler, J. (2012). Protein glycosylation as an adaptive response in Archaea: growth at different salt concentrations leads to alterations in *Haloferax volcanii* S-layer glycoprotein N-glycosylation. *Environ. Microbiol.* 14, 743–753. doi: 10.1111/j.1462-2920.2011.02625.x
- Henche, A. L., Ghosh, A., Yu, X., Jeske, T., Egelman, E., and Albers, S. V. (2012). Structure and function of the adhesive type IV pilus of *Sulfolobus acidocaldarius*. *Environ. Microbiol.* 14, 3188–3202. doi: 10.1111/j.1462-2920.2012.02898.x
- Hodgkin, J., and Kaiser, D. (1979). Genetics of gliding motility in *Myxococcus xanthus* (Myxobacterales): two gene systems control movement. *Mol. Gen. Genet.* 171, 177–191. doi: 10.1007/BF00270004
- Jarrell, K. F. (2012). Control of archaeellation in *Sulfolobus acidocaldarius*: unravelling of the regulation of surface structure biosynthesis in Archaea begins. *Mol. Microbiol.* 86, 1–5. doi: 10.1111/j.1365-2958.2012.08191.x
- Jarrell, K. F., and Albers, S. V. (2012). The archaeallum: an old motility structure with a new name. *Trends Microbiol.* 20, 307–312. doi: 10.1016/j.tim.2012.04.007
- Jarrell, K. F., Stark, M., Nair, D. B., and Chong, J. P. (2011). Flagella and pili are both necessary for efficient attachment of *Methanococcus maripaludis* to surfaces. *FEMS Microbiol. Lett.* 319, 44–50. doi: 10.1111/j.1574-6968.2011.02264.x
- Jarrell, K. F., Ding, Y., Nair, D. B., and Siu, S. (2013). Surface appendages of Archaea: structure, function, genetics and assembly. *Life* 3, 86–117. doi: 10.3390/life3010086
- Lassak, K., Ghosh, A., and Albers, S. V. (2012a). Diversity, assembly and regulation of archaeal type IV pili-like and non-type-IV pili-like surface structures. *Res. Microbiol.* 163, 630–644. doi: 10.1016/j.resmic.2012.10.024
- Lassak, K., Neiner, T., Ghosh, A., Klingl, A., Wirth, R., and Albers, S. V. (2012b). Molecular analysis of the crenarchaeal flagellum. *Mol. Microbiol.* 83, 110–124. doi: 10.1111/j.1365-2958.2011.07916.x
- Losensky, G., Vidakovic, L., Klingl, A., Pfeifer, F., and Fröls, S. (2014). Novel pili-like surface structures of *Halo bacterium salinarum* strain R1 are crucial for surface adhesion. *Front. Microbiol.* 5:755. doi: 10.3389/fmicb.2014.00755
- Moissl, C., Rachel, R., Briegel, A., Engelhardt, H., and Huber, R. (2005). The unique structure of archaeal “hami,” highly complex cell appendages with nano-grappling hooks. *Mol. Microbiol.* 56, 361–370. doi: 10.1111/j.1365-2958.2005.04294.x
- Nair, D. B., Chung, D. K., Schneider, J., Uchida, K., Aizawa, S., and Jarrell, K. F. (2013). Identification of an additional minor pilin essential for piliation

- in the archaeon *Methanococcus maripaludis*. *PLoS ONE* 8:e83961. doi: 10.1371/journal.pone.0083961
- Naor, A., Lapierre, P., Mevarech, M., Papke, R. T., and Gophna, U. (2012). Low species barriers in halophilic archaea and the formation of recombinant hybrids. *Curr. Biol.* 22, 1444–1448. doi: 10.1016/j.cub.2012.05.056
- Nather, D. J., Rachel, R., Wanner, G., and Wirth, R. (2006). Flagella of *Pyrococcus furiosus*: multifunctional organelles, made for swimming, adhesion to various surfaces, and cell-cell contacts. *J. Bacteriol.* 188, 6915–6923. doi: 10.1128/JB.00527-06
- Nather-Schindler, D. J., Schopf, S., Bellack, A., Rachel, R., and Wirth, R. (2014). *Pyrococcus furiosus* flagella: biochemical and transcriptional analyses identify the newly detected flaB0 gene to encode the major flagellin. *Front. Microbiol.* 5:695. doi: 10.3389/fmicb.2014.00695
- Nickell, S., Hergel, R., Baumeisiter, W., and Rachel, R. (2003). *Pyrodicticum* cannulae enter the periplasmic space but do not enter the cytoplasm, as revealed by cryo-electron tomography. *J. Struct. Biol.* 141, 34–42. doi: 10.1016/S1047-8477(02)00581-6
- Orell, A., Peeters, E., Vassen, V., Jachlewski, S., Schalles, S., Siebers, B., et al. (2013). Lrs14 transcriptional regulators influence biofilm formation and cell motility of Crenarchaea. *ISME J.* 7, 1886–1898. doi: 10.1038/ismej.2013.68
- Patenge, N., Berendes, A., Engelhardt, H., Schuster, S. C., and Oesterhelt, D. (2001). The *fla* gene cluster is involved in the biogenesis of flagella in *Halobacterium salinarum*. *Mol. Microbiol.* 41, 653–663. doi: 10.1046/j.1365-2958.2001.02542.x
- Peabody, C. R., Chung, Y. J., Yen, M. R., Vidal-Ingigliardi, D., Pugsley, A. P., and Saier, M. H. (2003). Type II protein secretion and its relationship to bacterial type IV pili and archaeal flagella. *Microbiology* 149, 3051–3072. doi: 10.1099/mic.0.26364-0
- Perras, A. K., Wanner, G., Klingl, A., Mora, M., Auerbach, A. K., Heinz, V., et al. (2014). Grappling archaea: ultrastructural analyses of an uncultivated, cold-loving archaeon, and its biofilm. *Front. Microbiol.* 5:397. doi: 10.3389/fmicb.2014.00397
- Pohlschröder, M., Ghosh, A., Tripepi, M., and Albers, S. V. (2011). Archaeal type IV pilus-like structures—evolutionarily conserved prokaryotic surface organelles. *Curr. Opin. Microbiol.* 14, 357–363. doi: 10.1016/j.mib.2011.03.002
- Reimann, J., Lassak, K., Khadouma, S., Ettema, T. J., Yang, N., Driessen, A. J., et al. (2012). Regulation of archaeal expression by the FHA and von Willebrand domain-containing proteins ArnA and ArnB in *Sulfolobus acidocaldarius*. *Mol. Microbiol.* 86, 24–36. doi: 10.1111/j.1365-2958.2012.08186.x
- Rosenshine, I., Tchelet, R., and Mevarech, M. (1989). The mechanism of DNA transfer in the mating system of an archaeobacterium. *Science* 245, 1387–1389.
- Shahapure, R., Driessen, R. P., Haurat, M. F., Albers, S. V., and Dame, R. T. (2014). The archaeellum: a rotating type IV pilus. *Mol. Microbiol.* 91, 716–723. doi: 10.1111/mmi.12486
- Streif, S., Staudinger, W. F., Marwan, W., and Oesterhelt, D. (2008). Flagellar rotation in the archaeon *Halobacterium salinarum* depends on ATP. *J. Mol. Biol.* 384, 1–8. doi: 10.1016/j.jmb.2008.08.057
- Syutkin, A. S., Pyatibratov, M. G., Galzitskaya, O. V., Rodriguez-Valera, F., and Fedorov, O. V. (2014). *Haloarcula marismortui* archaeellin genes as ecoparalogs. *Extremophiles* 18, 341–349. doi: 10.1007/s00792-013-0619-4
- Szabó, Z., Sani, M., Groeneveld, M., Zolghadr, B., Schelert, J., Albers, S. V., et al. (2007a). Flagellar motility and structure in the hyperthermoacidophilic archaeon *Sulfolobus solfataricus*. *J. Bacteriol.* 189, 4305–4309. doi: 10.1128/JB.00042-07
- Szabó, Z., Stahl, A. O., Albers, S. V., Kissinger, J. C., Driessen, A. J., and Pohlschröder, M. (2007b). Identification of diverse archaeal proteins with class III signal peptides cleaved by distinct archaeal prepilin peptidases. *J. Bacteriol.* 189, 772–778. doi: 10.1128/JB.01547-06
- Tripepi, M., Esquivel, R. N., Wirth, R., and Pohlschröder, M. (2013). *Haloferax volcanii* cells lacking the flagellin FlgA2 are hypermotile. *Microbiology* 159, 2249–2258. doi: 10.1099/mic.0.069617-0
- Tripepi, M., Imam, S., and Pohlschröder, M. (2010). *Haloferax volcanii* flagella are required for motility but are not involved in PibD-dependent surface adhesion. *J. Bacteriol.* 192, 3093–3102. doi: 10.1128/JB.00133-10
- Tripepi, M., You, J., Temel, S., Onder, O., Brisson, D., and Pohlschröder, M. (2012). N-glycosylation of *Haloferax volcanii* flagellins requires known Agl proteins and is essential for biosynthesis of stable flagella. *J. Bacteriol.* 194, 4876–4887. doi: 10.1128/JB.00731-12
- Vandyke, D. J., Wu, J., Ng, S. Y., Kanbe, M., Chaban, B., Aizawa, S., et al. (2008). Identification of a putative acetyltransferase gene, MMP0350, which affects proper assembly of both flagella and pili in the archaeon *Methanococcus maripaludis*. *J. Bacteriol.* 190, 5300–5307. doi: 10.1128/JB.00474-08
- Vassart, A., Van Wolferen, M., Orell, A., Hong, Y., Peeters, E., Albers, S. V., et al. (2013). Sa-Lrp from *Sulfolobus acidocaldarius* is a versatile, glutamine-responsive, and architectural transcriptional regulator. *Microbiologyopen* 2, 75–93. doi: 10.1002/mbo3.58
- Wang, Y. A., Yu, X., Ng, S. Y., Jarrell, K. F., and Egelman, E. H. (2008). The structure of an archaeal pilus. *J. Mol. Biol.* 381, 456–466. doi: 10.1016/j.jmb.2008.06.017
- Zolghadr, B., Klingl, A., Rachel, R., Driessen, A. J., and Albers, S. V. (2011). The bindosome is a structural component of the *Sulfolobus solfataricus* cell envelope. *Extremophiles* 15, 235–244. doi: 10.1007/s00792-010-0353-0
- Zolghadr, B., Weber, S., Szabó, Z., Driessen, A. J., and Albers, S. V. (2007). Identification of a system required for the functional surface localization of sugar binding proteins with class III signal peptides in *Sulfolobus solfataricus*. *Mol. Microbiol.* 64, 795–806. doi: 10.1111/j.1365-2958.2007.05697.x
- Zusman, D. R., Scott, A. E., Yang, Z., and Kirby, J. R. (2007). Chemosensory pathways, motility and development in *Myxococcus xanthus*. *Nat. Rev. Microbiol.* 5, 862–872. doi: 10.1038/nrmicro1770

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