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The upper temperature limit of life under hi h h dro tati pre ure in the deep io phere

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T T T

Keywords:
i h h dro tati pre ure
i h temperature
ie ophile
perthermophile
eep io phere

i h h dro tati pre ure i a ommon fa tor in the deep ea and pro ide an i nora le parameter of on ideration in all tudie related to deep life i h temperature en ironment in the deep ea maind in luding h drothermal ent and deep ediment in the u ea oor upport enormou amount of ioma produ ti it and di er it of life an mi ro e li in there are u uall h per thermophili pie ophile hi h ope ith the dual tre e of hi h temperature and at the ame time and pla in i ni ant role in eo hemi al elemental lin no led e of the upper temperature limit of life under deep ea ondition an help u to e timate the oundar of the io phere and e plore it ha ita ilit on arth and in e traterre trial area ut un ertaintie remain ere e ha e ummari ed the urrent no no led e of ph iolo i al orrelation et een hi h temperature and a ell a the effe t of on ell at hi h temperature The e effe t mainl ompri e t o a pe t iolo i al inte rit and meta oli fea i ilit The former ha een in e ti ated in man tudie on ariou mi roor ani m from hi h e an dra a eneral on lu ion that help ell maintain iolo i al inte rit under hi h temperature or the latter e i tin tudie ha e pro ided lue u e tin that oth hi h temperature and hallen e meta oli fea i ilit ut it i till dif ult to dra on lu ion on the additi e effe t on meta oli m due to the la of temati anal i ere e al o propo e a erie of ue tion for further in e ti ation and alled for more attention on meta oli re pon e to hi h tem perature and thi ould pro ide a dire t rid e et een eo hemi tr and e olo help u to under tand the mi ro ial fun tion in the deep io phere and allo u to e timate the oundarie of life and ha itat

1. Introduction

1.1. High hydrostatic pressure (HHP) is a common factor in the deep sea

ean o er more than of the arth' urfa e area and mi ro e ompri e appro imatel of the o ean ioma the are re arded a an important hidden dri er of e ential elemental lin e in the o ean arl una a a and ala ar ephton et al The deep ea refer to ater depth reater than m the h dro tati pre ure in rea e appro imatel a for e er m in rea e in ater depth the h dro tati pre ure in the deep ea i hi her than a hile in ediment the pre ure in rea e a per ilometer ari et al The a era e depth of o ean i m hi h pro ide an a era e h dro tati pre ure of appro imatel a anna h and Ta lor dro tati pre ure in uen e the ph iolo of or ani m li in in the deep ea hi h i the lar e t ha itat of the io phere in term of olume × m hitman et al n eneral deep ea pro ar ote are no n to e predominantl pie ophili that mean adapted to hi h h dro tati pre ure ondition Tam urini et al t i elie ed that io tope under ele ated pre ure repre ent the lar e t ha itat for mi ro ial life on arth and pre ure enerall enhan e mi ro ial a ti it rate in deep en ironment i ard and aniel a pioneer in pie ophile tudie artlett and hi olla orator ha e done a lot of or on ho impa t the iolo i al pro e e in p hrophili pie ophili a teria in e ti atin the han e of repli ation ene e pre ion and re ulation re pirator tem a ellar tem and eneti mu tation under Tame ai et al l a et al arietou et al loe et al auro et al The e or indi ated the importan e of un aturated fatt a id proportion and in rea in immin elo it under in a ell tudied p hrophili pie o phili a teria train *Photobacterium profundum* lthou h their

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or in train ho ed that the re pirator omponent a not affe ted altered pre ure the ame up an a umption that train ma u e fermentation rather than re piration under hi h pre ure Tame ai et al n addition an et al reported han e in the ener ield of redo rea tion in the deep ea under lo temperature and ondition and ompared the e ondition to tho e of urfa e en ironment at ° and a an et al n re ent tudie a reported to impa t the hift of end produ t of fermentation and e ternal ele tron a eptor in re piration in oth the mi ro iolo i al ommunit and in pure ultured train a of ediment are armer than ° and of marine edi ment are armer than ° aro e et al on iderin the m a era e depth of o ean ith pre ure of a and the litho tati pre ure found ith in rea in depth of ediment and ru t er and e ar mi ro e in the u ea oor often en ounter and mu t ur i e ondition of hi h h dro tati pre ure hi h temper ature and ometime e treme tar ation o uet eople et al o e er the u ea oor io phere i till u e ted to ontain t o third of arth' total pro ar oti ioma hitman et al t i no n that u ea oor mi ro e pla a i ni ant role in hemi al rea tion that ere pre iou l thou ht to ha e een a ioti in ludin iron and ulfur lin a ell a ethane and propane eneration in ri h et al o e er the limit of u urfa e life in term of an en ironmental propertie are not et no n due to the la of te ta le ulture

1.3. *What is the upper temperature limit for life under HHP?*

the re ord for the deepe t ediment ha een rai ed e eral time the re ord for edimentar mi roor ani m li in at hi h temperature ha al een updated ou el et al euer et al i n ou el et al pro ided e iden e of pro ar oti ell li in m elo ea oor m f ediment at temperature of – ° and u e ted that repre entati e h perthermophile Thermo o ale i e *Thermococcus* and *Pyrococcus* i the onl roup a ti e in the deep io phere at that depth ou el et al n a re ent tud euer et al pro ided e iden e for ro in mi ro e li in up to a depth of m ith hot ediment up to ° in the an ai Trou h u du tion one The mi ro iolo i al meta oli a ti itie are di tin ui hed different temperature one o e ° to – ° the iolo i al produ tion and o idation of methane are dete ted hile at ° – ° the a ti it of a etate de radin h perthermophile i dete ted The e re ult u e ted that temperature i one of the e fa tor hapin the meta oli pro e e o urrin in deep ediment and further ho that life in the deep u ea oor i not on trained an upper temperature limit elo ° euer et al

or pure ultured mi ro e the re ord for the hi he t ro th tem perature ha een rai ed e eral time in the pa t e de ade Ther mophile ere r t di o ered in the hot prin of ello tone ational ar in the nited tate and their hi he t ro th tempera ture ould e a hi h a ° hi h a re orded a for hloroph lle *Schizomycetes* in et hell Thermophili a teria ith a ma imum ro th temperature of ° ere di o ered in the and ro ith the di o er of h drothermal ent in the h perthermophile ho e ma imum ro th temperature e eeded ° ere i olated there aro et al Thi i the r t time it a reali ed that the upper temperature of life an rea h °

Thu far mi ro e ith the a ilit to ro at and a o e appro imatel ° are all ar haea ro an n a *Pyrolobus fumarii* train

1

eported h per thermophili pie ophile in ludin_ oth a teria and ar haea re iation Topt optimal _ro th temperature Tma ma imum _ro th temperature opt optimal _ro th pre ure deep ea h drothermal ent deep ea h drothermal ediment and _eothermall heated ea oor no data

T pe	train name	a itat	*in situ* depth m	Topt °	Tma °	opt a	ran_e a	ner_ meta oli m	eferen e
a teria	*Anoxybacter fermentans*			–			–	e + redu tion	en_ et al
	Piezobacter thermophilus						–	o idation	Ta ai et al
	Thioprofundum lithotrophica						–	o idation	Ta ai et al
	Thermosipho japonicus						–	redu tion	Ta ai and ori o hi
	Marinitoga piezophila						–	redu tion	lain et al
	Pseudothermotoga elfii DSM9442		–				–	ermentation	ouma_na et al a ot et al
	Clostridium paradoxum		–	a	a a		–	ethano_ene i	i et al oma et al
r haea	*Methanocaldococcus jannaschii*			a a a			– [a]	ethano_ene i	one et al oon aratana orn it
	Methanococcus thermolithotrophicus						–	ethano_ene i	u er et al
	Methanopyrus kandleri				a a a		–	ethano_ene i	urr et al Ta ai et al
	Methanopyrus kandleri							e + redu tion	a he and o le
	Palaeococcus ferrophilus						–	redu tion	Ta ai et al
	Palaeococcus pacificus						–	redu tion	en_ et al
	Pyrococcus abyssi				a a		–	redu tion	rau o et al
	Pyrococcus yayanosii				a a		–	redu tion	irrien et al
	Thermococcus aggregans T						–	redu tion	an_anella et al
	Thermococcus guaymasensis T					–	–	redu tion	an_anella et al
	Thermococcus peptonophilus						–	redu tion	on ále et al
	Thermococcus eurythermalis				a a	– ° °	–	redu tion	hao et al
	Thermococcus barophilus				a a		–	redu tion	artein on et al
	Thermococcus paralvinellae				a a			redu tion	en le et al
	Thermococcus piezophilus				a		–	redu tion	alma o et al
	Thermococcus barophilus h							redu tion	_er et al han_ et al
	Thermococcus camini Iri35c			–		–	–	redu tion	ourtine et al
	Pyrococcus train				a a			redu tion	olden and aro
	Pyrococcus p				a			redu tion	anna h et al
	Desulfurococcus p				a a			redu tion	anna h et al
	Archeoglobus fulgidus	heated ea oor			a	–	–	ulfate redu tion	li er et al tetter

re iation Topt optimal _ro th temperature Tma ma imum _ro th temperature opt optimal _ro th pre ure deep ea h drothermal ent deep ea h drothermal ediment and _eothermall heated ea oor deep oil produ in_ ell no data

[a] or *M. jannaschii* train a orre pond to the hi_he t pre ure te ted ith a hi_her _ro th rate ut the optimum pre ure i not no n iller et al

them to maintain and survive. The current °C record at a provides a potential opportunity to investigate the upper temperature limit of life considering the effect of

The optimal growth temperature of microorganisms has been proved to be closely related to the nucleic acid sequence of the genome (Sauer et al.,) using statistical and machine learning methods. Li et al. developed software that uses protein sequences annotated from the complete genome to predict the optimal growth temperature of microorganisms (Li et al.,). This software can accurately predict the optimum growth temperature from the microbial dipeptide sequence, and the catalytic temperature of an enzyme can be predicted for the sequent amino acid sequence of the individual enzyme. We used this method to predict the optimal growth temperature of some piezophilic hyperthermophiles mentioned above (Table). The software gave overall accurate predictions, but when the experimental optimum growth temperature was over °C, especially °C, a – °C deviation was observed. On the one hand, the deviation may be caused by a larger value of the optimum growth temperature; on the other hand, thermophiles with optimum growth temperature over °C may have a special thermal stability mechanism. In addition to the stability of the protein structure of large molecules, there are other mechanisms favoring adaptation to the high temperature environment. Using the training set data model and the microbial optimal growth temperature prediction model of the software, one can in theory adjust the software to predict the relationship of microbial maximum growth temperature. By replacing the training data set, but the optimum growth temperature and the highest temperature of the microorganism do not exhibit a linear relationship yet, even which means that the highest temperatures of microorganisms are not completely determined by the genome. Therefore, the software predictions of the temperature adjustment needed to obtain the highest growth temperature may not be completely accurate.

. to maintain biologic integrity at high temperature

In this section, we review the knowledge and potential puzzles arising from studies on water chemistry, the stability of cell membranes and macromolecules, and the synthesis and accumulation of molecular chaperones and compatible solutes under high temperature, and in these situations, some negative impacts on cells and cellular components caused by high temperature.

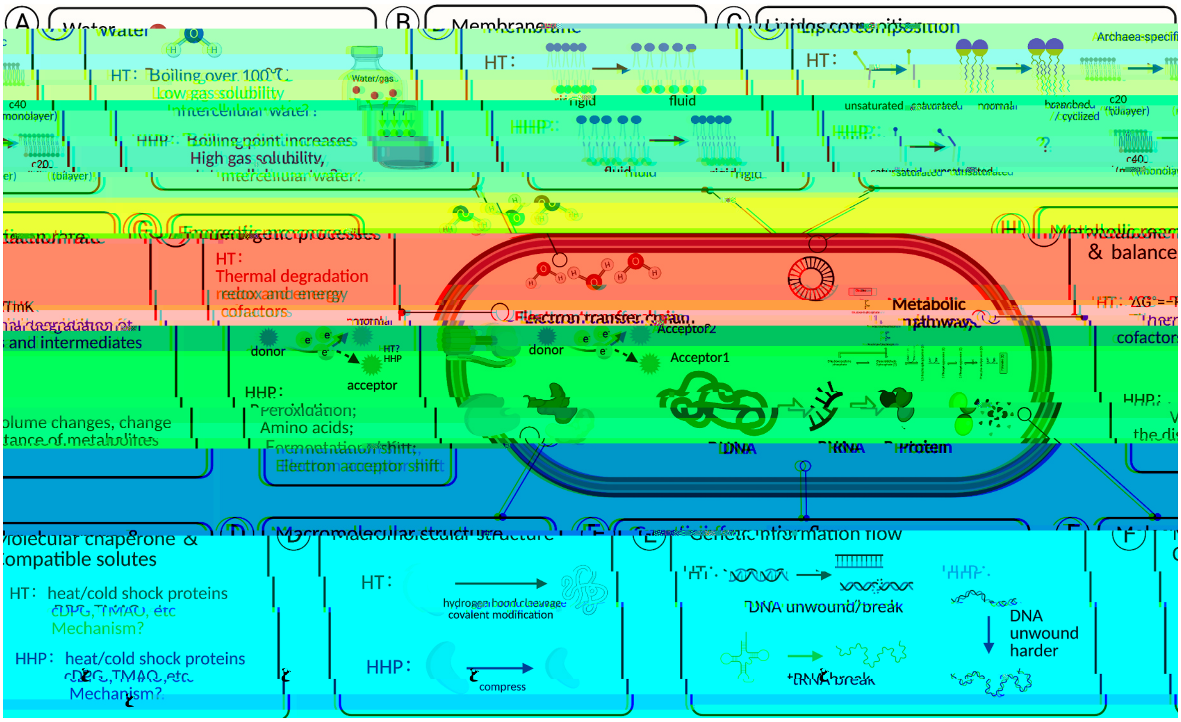

Fig. . Schematic diagram of the effect of high temperature and high hydrostatic pressure on cell and biological processes in hyperthermophilic piezophiles. (HT: high temperature; HHP: high hydrostatic pressure.)

relaxation dynamics in this hyperthermophilic protein than in a mesophilic model protein. High pressure provides evidence that the protein energy landscape is distorted by high pressure and is significantly different for hyperthermophilic and mesophilic proteins (Shrestha et al.,). Tros et al. () used ultrafast infrared spectroscopy and dielectric relaxation spectroscopy to observe the random orientational motion of water molecules inside the living cells of three prototypical mesophilic organisms. They found that most of the intracellular water exhibited the same random orientational motion as neat water, whereas a smaller fraction (–%) exhibited slower orientational dynamics. This intercellular slow water is proposed to bound primarily to proteins and, to a lesser extent, to other biomolecules and ions (Tros et al.,). In addition, the high flexibility of proteome associated with reduced hydration water was observed in hyperthermophilic piezophilic archaea using quasi-elastic neutron scattering, which was proposed to be a potential key to the molecular adaptation of the cells to high hydrostatic pressure (Martinez et al.,). However, the detailed physical effect of temperature and/or pressure on intercellular water in both mesophilic and hyperthermophilic conditions remains a mystery.

3.2. Cell membrane

The cell membrane is essential for separating the intracellular environment from the outside. The existence of the membrane enables the cell to maintain a relatively stable internal environment to support biological functions in the face of changing or extreme external environment. The mobility of the cell membrane increases at high temperature (Li,), with the application of lethal heat stress; the high mobility of the cell membrane easily leads to the appearance of pores and structural damage, which causes solute outflow and cell lysis. In addition, lethal heat stress also has a great impact on binding of membrane proteins and the permeability of cell membranes. At lethal high temperature, membrane proteins aggregate, membrane protein activity decreases, solute flux decreases, and the permeability of cations increases (Lande and).

Hyperthermophiles themselves have special membrane properties allowing them to adapt to high growth temperature. For example, thermophilic bacteria enhance the thermal stability of membrane by increasing the proportion of saturated fatty acids in phospholipid molecules, increasing the length of phospholipid alkyl chains and increasing the proportion of isomerized branched chains (mana a,). Hyperthermophilic archaea use a monolayer membrane structure comprising glycerol dibiphytanyl glycerol tetraether (GDGT), which are more rigid and impermeable than classical bacterial/eukaryal bilayer membranes made of diacylglycerol. GDGTs impart higher mechanical strength to resist the high temperature environment (Chong,). In addition, the increase in cyclopentane structure and the glycosylation modification of the glycerol skeleton are also ways for hyperthermophilic archaea to maintain the stability of membranes (Ulrih et al.,). Most of these adaptation mechanisms enhance stability through changing membrane lipids and their composition.

Generally, help maintain membrane integrity, fluidity and permeability, like the low temperature treatment leading to contrasting results at high temperature (Li,) and low temperature can both make the cell membrane orderly and compress the packing of fatty acids (Daniel et al.,). At MPa and °, the fluidity of the membrane is similar to that seen at – ° under a pressure of MPa (Simonato et al.,). Each MPa increase in pressure is equivalent to a – ° decrease in temperature, but the exact equivalence is determined by the composition of the lipid system (Somero,). High temperature increases the entropy of the membrane and increases its disorder, while high pressure will reduce the entropy. The increase in pressure reduces the fluidity of the membrane, so can maintain the fluidity of the membrane within a relatively stable range. For membrane proteins, on the one hand, as mentioned above, the increase in hydrostatic pressure is conducive to the maintenance of the protein's structure to a certain extent, so can maintain the protein's higher structure resisting the damage caused by high temperature. On the other hand, due to the increased accumulation of lipid chains, can cause changes in protein-membrane interaction (arlata,). The influence of on the membrane structure can maintain the stability of the membrane and the normal function of the membrane when thermophile are u e ted to lethal thermal tre and thi i one of the a that an in rea e the ma imum temperature and maintain the inte rit of the ell tru ture

lmo t all ar haea produ e oth diether and tetraether Tourte et al er and ario an or to date ha e demon trated a tron orrelation et een the diether tetraether ratio in lipid ompo ition and adaptation to ariou e treme ondition in addition to hi h temperature u h a e treme a idit al alinit alinit and o d et al ate ario et al ario et al mea ured the ratio of diether r haeol er u tetraether T under different temperature and pre ure i Their re ult learl ho ed the imilar trend ith in rea in pre ure and de rea in temperature oth of hi h led to an in rea e in the pro portion of diether on er el a hi her proportion of T a o er ed under lo pre ure and hi h temperature ondition ota l u tuation in pre ure and temperature al o impa ted the le el of un aturation of apolar lipid ith an irre ular pol i oprenoid ar on eleton un aturated l opane deri ati e ario et al i

3.3. Macromolecules

an iomole ule e pe iall the ma romole ule fa e different threat under heat tre The effe t of hi h temperature on iolo i al ta ilit i the mo t tudied of the e threat dro en ond i a ind of ea intera tion and h dro en ond in protein help to ta ili e pro tein tru ture teiner or protein mole ule irre er i le dena turation o ur hen the h dro en ond in ide the protein are ro en under the in uen e of deadl thermal tre harna l et al t the ame time amino a id re idue in protein mole ule are prone to under o o alent modi ation at hi h temperature leadin to the ina ti ation and de radation of protein mole ule u h a in the dea midation of lutamine re idue and a para ine re idue and the o ida tion of teine re idue aeni e and terner i The nu lei a id mole ule and are al o threatened hi h tem perature The dou le heli of the mole ule ill open hen the temperature e eed the meltin temperature and the tru ture of the t mole ule i ea il de tro ed at hi h temperature aeni e and terner and it annot parti ipate in the fun tional tran lation pro e i

perthermophile e hi it pe ial adaptation me hani m for adaptin to “optimal ro th” temperature ondition u h a enhan in non o alent for e ittle hild et al impro in the ta ilit of α heli e terner and ie l and redu in h dropho i effe t olden and aniel o e er hen h per thermophile fa e nearl lethal thermal tre the e hi h temperature adaptation me hani m annot effe ti el maintain the fun tional a ti itie of ell n thi enario an help maintainin the ta ilit of the e iomole ule to ome e tent or e ample ere et al found that hi h pre ure an help maintainin the ta ilit of h dro ena e of *M. jannaschii* a ed on their re ult thi effe t a propo ed to pla a role e ta li hin h dropho i intera tion The author al o anal ed ho helped to maintain the internal pa a in of amino a id to pre er e ta ilit ei and lar promote protein ompre ion and miti ate the dama e of the three dimen ional tru ture au ed the lo of protein h dro en ond indu ed hi h temperature el h et al dditionall help ta ili e the tru ture of and deal with the cell damage caused by lethal heat stress. The accumulation of multiple compatible solutes and their *de novo* biosynthetic pathways have been identified and shown to be associated with various stresses, but little is known about their *in vivo* physiological and metabolic roles, which leaves a huge knowledge gap in our understanding of how compatible solutes work in cells. It deserves to extend studies on more hyperthermophilic microorganisms from the deep biosphere.

. ot i t r tur nd c n t t o ic i i it

Hyperthermophilic microorganisms are all chemotrophic microorganisms, including chemoautotrophs and chemoheterotrophs. The chemoautotrophic microorganisms are mainly anaerobic and a few are microoxygenated. They carry out energy metabolism through the oxidation of and as well as the reduction of $^{-}$ and $^{-}$ (hönheit and hönheit). The metabolic pathways of chemoheterotrophic hyperthermophiles mainly include the metabolism of peptides and sugars as substrates. Their energy metabolism is very diverse and involves the use of different kinds of electron acceptors, such as $^{+}$, $^{-}$, sulfur compounds in different oxidation states and even protons (hönheit and hönheit). Some of them contain more than one electron acceptor in the electron transfer chain. With the presence of external electron acceptors, the substrates will be oxidized to and/or converted to other organic products with low molecular weights (e.g., acetate, propionate, alcohol) by fermentation (hönheit and hönheit). Hyperthermophiles have special characteristics in their metabolic pathways to address challenges of thermal stresses, but they still suffer from chemical reaction imbalance, accumulation of toxic metabolites, and loss in coupling efficiency caused by temperature disturbance. Similarly, also has global impacts on metabolism as mentioned from the very beginning. Therefore, the dual stress conditions of high temperature and will cause additive influence on metabolism. In this section, we summarized the reported challenges and potential annier et al ario et al o er ed more amino a id re uirement in a h perthermophili pie ophile under and h poth e i ed that the lo ener ield of fermentation of or ani pol mer to ether ith ener et on traint impo ed hi h h dro tati pre ure ma render *de novo* nthe i of amino a id e olo i all unfa ora le ario et al e ardle it i till too earl to dra on lu ion on ho hi h temperature and impa t meta oli m and temati in e ti ation of the intera tion et een the e t o fa tor are till in uf ient e pe iall ith re pe t to the uantitati e anal i needed to hed li ht on ho hi h temperature and impa t meta oli m indi iduall and ho ooperati el

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Temperature i on idered the e limit for life and ha itat The di o er of life in hi h temperature en ironment in the deep ea i e h drothermal ent and deep u ea oor profoundl e tended our ie of the oundar of oth life and the ha itat en ironment of the arth ith the re o nition of the i ni ant impa t of on e the a in hi h e ie the ph i al ph iolo i al and meta oli pro le of life li in in the deep ea and deep io phere ha al o een han ed e pite the relati el lear and ontra tin effe t of hi h temperature and on iolo i al inte rit our no led e of meta oli re pon e ha man lind area pot e en ith re pe t to the indi idual ffe of either hi h temperature or not to mention the me hani m of o tre adaptation o e er meta oli m ma pro ide a dire t rid e et een eo hemi tr and e olo The urrent no led e ap re ardin meta oli m limit our under tandin of the real mi ro iolo i al fun tion mediatin the elemental le under *in situ* pol e treme en ironment in the deep ea and hinder our e timation of here the oundarie for oth life and ha itat are lo ated

a ed on the no led e re ie ed a o e durin the e ploration of the upper temperature limit of life and the orrelation et een hi h temperature and e rai e a erie of ue tion re uirin further in e ti ation there an on er ent e olution in meta oli m under hi h temperature and or if o hi h path a in ludin oth fermentation and re piration are fa ora le hat' the nal effe t under oth hi h temperature and here i the real upper temperature limit of life and hi h or ani m ill hold the ne t re ord

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The author are upported the follo in fundin our e the atural ien e oundation of hina rant num er and " ou le ir t la " initiati e

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e ' ploration of the effe t of hi h h dro tati pre ure on mi ro ial ro th ph iolo and ur i al per pe ti e from pie oph iolo io i iote hnol io hem –
lain artein on T iro hni hen o li a eta irrien '*Marinitoga piezophila* p no rod haped thermo pie ophili a terium i olated under hi h h dro tati pre ure from deep ea h drothermal ent nt t ol i ro iol –
aro ille ordon ' the and entin from u marine h drothermal tem produ ed thermophili a teria ature –
artlett ' re ure effe t on in i o mi ro ial pro e e io him ioph ta rotein tru t ol n mol –
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o d amilton T an iu han 'The role of tetraether lipid ompo ition in the adaptation of thermophili ar haea to a idit ront i ro iol arti le
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ario e ar Thiel er are er ' ole ular haperone a umulation a fun tion of tre e iden e adaptation to hi h h dro tati pre ure in the pie ophili ar haeon *Thermococcus barophilus* i ep
ario ormière iao er a h h dro tati pre ure in rea e amino a id re uirement in the pie o h perthermophili ar haeon *Thermococcus barophilus* e i ro iol –
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hon ein han T inter ' tru ture and onformation of ipolar tetraether lipid mem rane deri ed from thermoa idophili ar haeon *Sulfolobus acidocaldarius* a re ealed mall an le ra atterin and hi h pre ure T pe tro op h hem –
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hon a indra hurana n li h inter ' re ure pertur ation and differential annin alorimetri tudie of ipolar tetraether lipo ome deri ed from the thermoa idophili ar haeon *Sulfolobus acidocaldarius* ioph –
onnell ople T urton tan eld T ler erman an o er mon urlon rindla a man uhner a h ud e e a T hail eier a amura e e od eder en lou ie and earle te en on Ta il o ' drothermal ent eld and hemo ntheti iota on the orld' deepe t ea oor preadin entre ature ommunni ation
ourtine in e ai nien hilippon a et hao lain '*Thermococcus camini* p no h perthermophili and pie ophili ar haeon i olated from deep ea h drothermal ent at the mid atlanti rid e nt t ol i ro iol
alma o er el a ourtine aridon arla helli ou el i a a i e eillaud e ar Ta ai ai nien lain '*Thermococcus piezophilus* p no a no el h perthermophili and pie ophili ar haeon ith a road pre ure ran e for ro th i olated from a deepe t h drothermal ent at the id a man i e t ppl i ro iol –
aniel er inter ' ri in of life and io hemi tr under hi h pre ure ondition hem o e –
aniel o an ' iomole ular ta ilit and life at hi h temperature ell ol ife i –
i ana a e apa a ata ' odellin of h drothermal ent plume to a e the mineral parti le di tri ution draul e

pre ure ' *zvestiya vysshikh uchebnykh zavedenii* eri a himi a i himi he a a Te hnolo i a –

on ále ato ori o hi '*Thermococcus peptonophilus* p no fa t ro in e tremel thermophili ar hae a terium i olated from deep ea h drothermal ent r h i ro iol –

orla oonin ien enu rieur e lin 'T the r t iru i olated from the h perthermophili enu *Thermococcus* n iron i ro iol –

ro an n treme Thermophile n e ohn ile & on td hi he ter

a hi u a ato T tomi % .' eta oli m dealin % A0 0 thermal de radation of + in the h perthermophili ar haeon *Thermococcus kodakarensis* a teriol

artl artin ' ole ular haperone in ellular protein foldin urr pin tru t iol –

ei lar ' re ure ta ili ation of protein from e treme thermophile ppl n iron i ro iol –

en le un ar olden '*Thermococcus paralvinellae* p no nd *Thermococcus cleftensis* p no f h perthermophili heterotroph from deep ea h drothermal ent nt % t- ol 0 i ro iol –

euer na a i orono u o pi a ieh e er Treude T euli hu ot Tonai o den ramm en el iro e T omola o hino T iri ma hi ami a ane o a o tina anner lelland et alfe ut u an aud epp au a e T an an T hita er amamoto an aeda dhi ari lom it a amada allme er endt örmer % 0 amada ino hita inri h Temperature limit to deep u ea oor life in the an ai Trou h u du tion one ien e –

inri h a e a h pi a melo olm ohn on l a ' iolo i al formation of ethane and propane in the deep marine u urfa e ro atl ad i % > B B

ofmann irt antia o h el i o ohl ' tru ture elu idation of the thermal de radation produ t of the nu leotide ofa tor and nano T and nal ioanal hem –

tl

ou el ona ita uerellou ra_ _ e ter rieur ar e ' tendin_ the u ea oor io phere ien e

al ador a tell olu artine lli ier eter _er The r t tud on the impa t of o mol te in hole ell of hi_h temperature adapted mi roor_ani m oft atter –

anto o ta ' ompati le olute of or_ani m that li e in hot aline en ironment n iron i ro iol –

anto amo a aria T o_e e e 'The ph iolo_i al role io nthe i and mode of a tion of ompati le olute from h per Thermophile n erda lan dorff d h iolo_ and io hemi tr of tremophile meri an o iet of i ro iolo_

a ar e ' u ea oor ediment an e treme ut_lo all i_ni ant pro ar oti ha itat ta onom di er it e olo_ n ori o hi d tremophile and oo prin_er To o

auer an_ alen ia redi tin_ the optimal _ro th temperature of pro ar ote u in_ onl _enome deri ed feature ioinformati _

arlata The effe t of h dro tati pre ure on mem rane ound protein ra ed iol e –

harna_l eif riedri h ' ta ilit of protein temperature pre ure and the role of the ol ent io him ioph ta iomem r –

hönheit häfer T ' eta oli m of h perthermophile orld i ro iol iote hnol –

oma arrido mador iel en ø eld en The pol e tremophili a terium *Clostridium paradoxum* attain pie ophili trait modulatin_ it ener_ meta oli m and ell mem rane ompo ition pplied n ironmental i ro iolo_ eport

ephton aite ro ell T ' o to dete t life on i moon tro iolo_ –

et hell ' pper temperature limit of life ien e –

hre tha ho mi ople T a_i eo hu ' ffe t of pre ure on the d nami of an oli_omeri protein from deep ea h perthermophile ro atl ad i –

imonato ampanaro auro e i i hela ' itulo alle artlett ' ie ophili adaptation a _enomi point of ie iote hnol –

omero ' daptation to hi_h h dro tati pre ure nnu e h iol –

taudi_el Treati e on _eo hemi tr h drothermal alteration pro e e in the o eani ru t Treati e on _eo hemi tr –

teiner T The h dro_en ond in the olid tate n_e hem nt d –

terner ie l 'Thermophili adaptation of protein rit e io hem ol iol –

tetter '*Archaeoglobus fulgidus* _en o p no a ne ta on of e tremel thermophili ar hae a teria t ppl i ro iol –

tetter ' i tor of di o er of the r t h perthermophile tremophile –

una_a a ala ar arine mi ro ial di er it urr iol –

Ta ai ori o hi '*Thermosipho japonicus* p no an e tremel thermophili a terium i olated from a deep ea h drothermal ent in apan tremophile –

Ta ai i a a i ira ama a a_a a uerellou odfro ' olation and ph iolo_i al hara teri ation of t o no el pie ophili thermophili hemolithoautotroph from a deep ea h drothermal ent himne n iron i ro iol –

Ta ai a amura To i T T uno_ai i a a i i a a i ira ama a a_a a unoura T ori o hi ' ell proliferation at ° and i otopi all hea produ tion h perthermophili methano_en under hi_h pre ure ulti ation ro atl ad i –

Ta ai u_ai toh T ori o hi '*Palaeococcus ferrophilus* _en o p no arophili h perthermophili ar haeon from deep ea h drothermal ent himne nt t ol i ro iol –

Tam urini outrif arel ol ell emin_ ro ar oti e pon e to dro tati re ure in the ean – e ie ol pp –

Tame_ai i hi a a a_a artlett The re pirator tem of the pie ophile *Photobacterium profundum* _ro n under ariou pre ure io i iote hnol io hem –

Tourte haeffer ro i _er ' un tionali ed mem rane domain an an e tral feature of ar haea ront i ro iol

Tro hen_ un_er onn onn mit outer en ' i o e ond orientational d nami of ater in li in_ ell ' at ommun

lrih ma ner a por ' tru tural and ph i o hemi al propertie of polar lipid from thermophili ar haea ppl i ro iol iote hnol –

annier i houd _er artein on e ar enome e pre ion of *Thermococcus barophilus* and *Thermococcus kodakarensis* in re pon e to different h dro tati pre ure ondition e i ro iol –

an_ han_ artlett iao 'Tran riptomi anal i re eal ommon adaptation me hani m under different tre e for moderatel pie ophili a teria i ro ol –

el h T are ell eidhardt artlett ' tre re pon e of *Escherichia coli* to ele ated h dro tati pre ure a teriol –

hitman oleman ie e ' ro ar ote the un een ma orit ro atl ad i –

il o ellular on e tion model of mid o ean rid_e h drothermal ir ulation and the temperature of la mo er uid ournal of eoph i al e ear h tmo phere

iao han_ an_ ' dro tati pre ure i the uni er al e dri er of mi ro ial e olution in the deep o ean and e ond n ironmental i ro iolo_ eport –

ie ian in iao nhan in_ the adapta ilit of the deep ea a terium *shewanella piezotolerans* to hi_h pre ure and lo temperature e perimental e olution under tre ppl n iron i ro iol e

an_ iu an_ an an_ oon an_ iao han_ ' enomi and en mati e iden e of a eto_ene i anaero i methanotrophi ar haea at ommun

in han_ i han_ ian_ T i hen antini hou hou u ' i_h h dro tati pre ure indu i le trimeth lamine o ide redu ta e impro e the pre ure toleran e of pie o en iti e a teria *Vibrio fluvialis* ront i ro iol

en han_ ian_ lain e ar hao '*Palaeococcus pacificus* p no an ar haeon from deep ea h drothermal ediment nt t ol i ro iol –

en_ han_ i han_ ao e ar lain hao '*Anoxybacter fermentans* _en o p no pie ophili thermophili anaero i fermentati e a terium i olated from deep ea h drothermal ent nt t ol i ro iol –

han_ ian_ i T u iu on_ _er ' hara teri ation of a no el t pe al ohol deh dro_ena e from *Thermococcus barophilus* h nt iol a romol –

hao a iu ian han_ iao ' ro tre adaptation in a pie ophili and h perthermophili ar haeon from deep ea h drothermal ent ront i ro iol

hao en_ iao 'Thermo o u eur thermali p no onditional pie ophili h perthermophili ar haeon ith ide temperature ran_e for _ro th i olated from an oil immer ed himne in the _ua ma a in nternational ounral of temati nd olutionar i ro iolo_ –

ieren er_ dam rp ' ife in e treme en ironment h drothermal ent ro atl ad i nit tate m –