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Sarah Temmam, Khamsing Vongphayloth, Eduard Baquero Salazar, Sandie Munier, Massimiliano Bonomi, Béatrice Regnault, Bounsavane Douangboubpha, Yasaman Karami, Delphine Chrétien, Daosavanh Sanamxay, et al.

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# De nouveaux coronavirus de chauve-souris similaires à SARS-CoV-2 éclairent l'origine de la pandémie de COVID-19.

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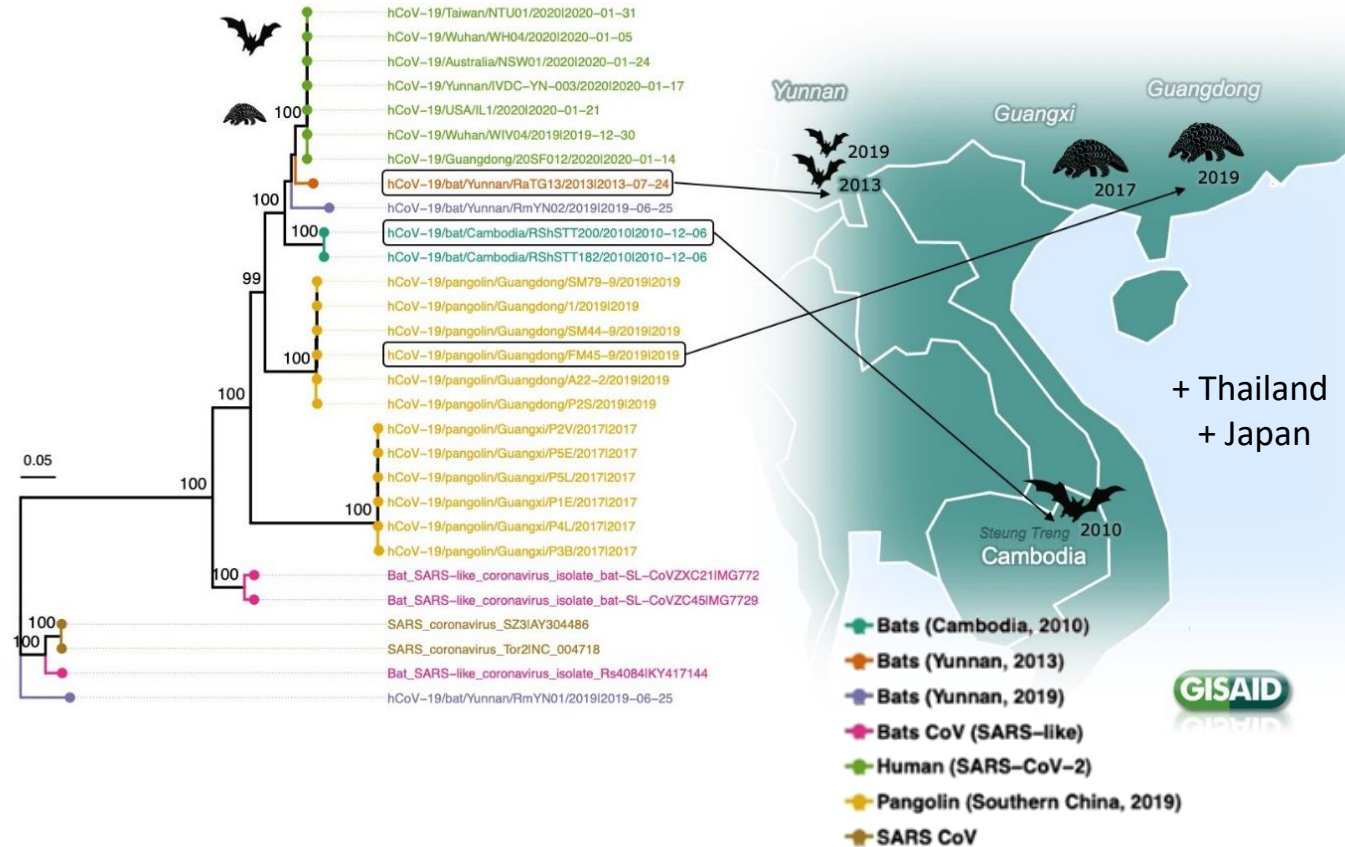
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\* co-first authors

+ corresponding author

# Context

- Numerous SARS-CoV-2-related viruses identified in **bats & pangolins**
- First cases detected in **Wuhan** (Huanan seafood market & elsewhere) *Worobey M. 2021 Science*
- First case 8<sup>th</sup> **December 2019**



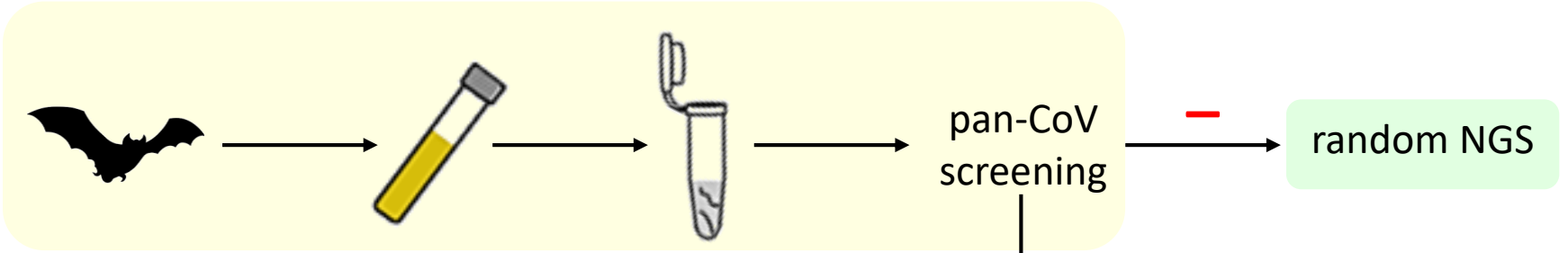
- Animal reservoir?
- Intermediate host?
- Routes of introduction into human populations?
- Silent circulation in humans before detection?

# Objectives

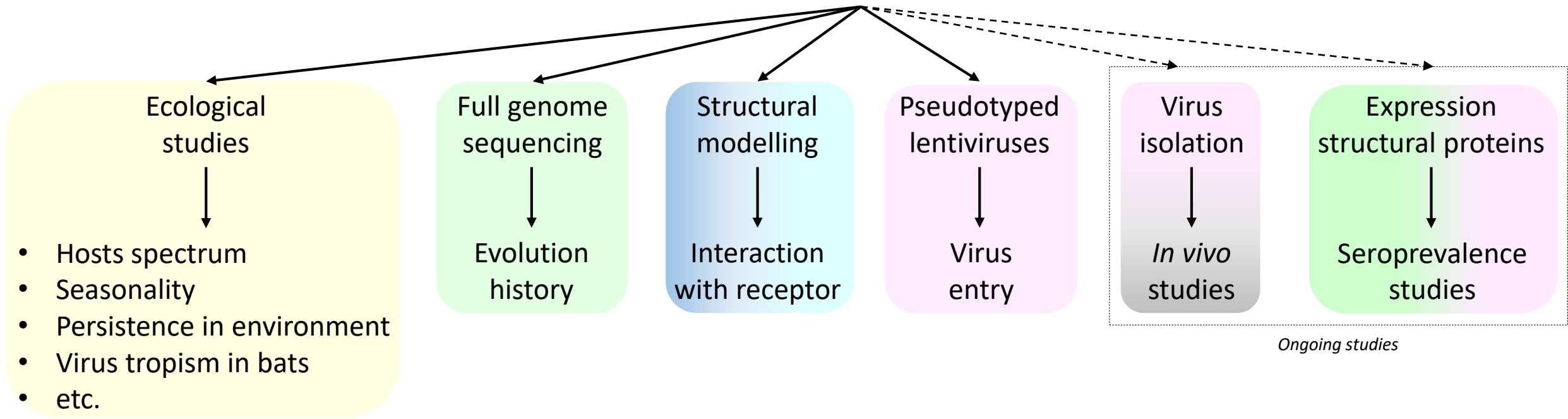
- To improve the understanding of the **origins, natural history** and **dissemination** of SARS-CoV-2 and SARS-like coronaviruses **in their natural environment**
    - Identify natural reservoir(s) of SARS-CoV-2
    - Decipher interspecies transmission (bat-to-bat, bat-to-mammals, bat-to-humans)
  - To detect **past coronavirus infections** in humans exposed to animal reservoirs
    - Identify early circulation of SARS-CoV-2 or SARS-CoV-2-like viruses before global spread
- Ecological factors that lead to SARS-CoV-2 emergence

# Workflow & consortium

- IP-Laos
- IPP-Pathogen discovery
- IPP-Structural virology
- IPP-Structural bioinformatics
- IPP-Molecular Genetics of RNA Viruses
- IPP-Mouse genetics



## Characterization of the virus





# Field work



Khamsing  
Vongphayloth  
IP-Laos



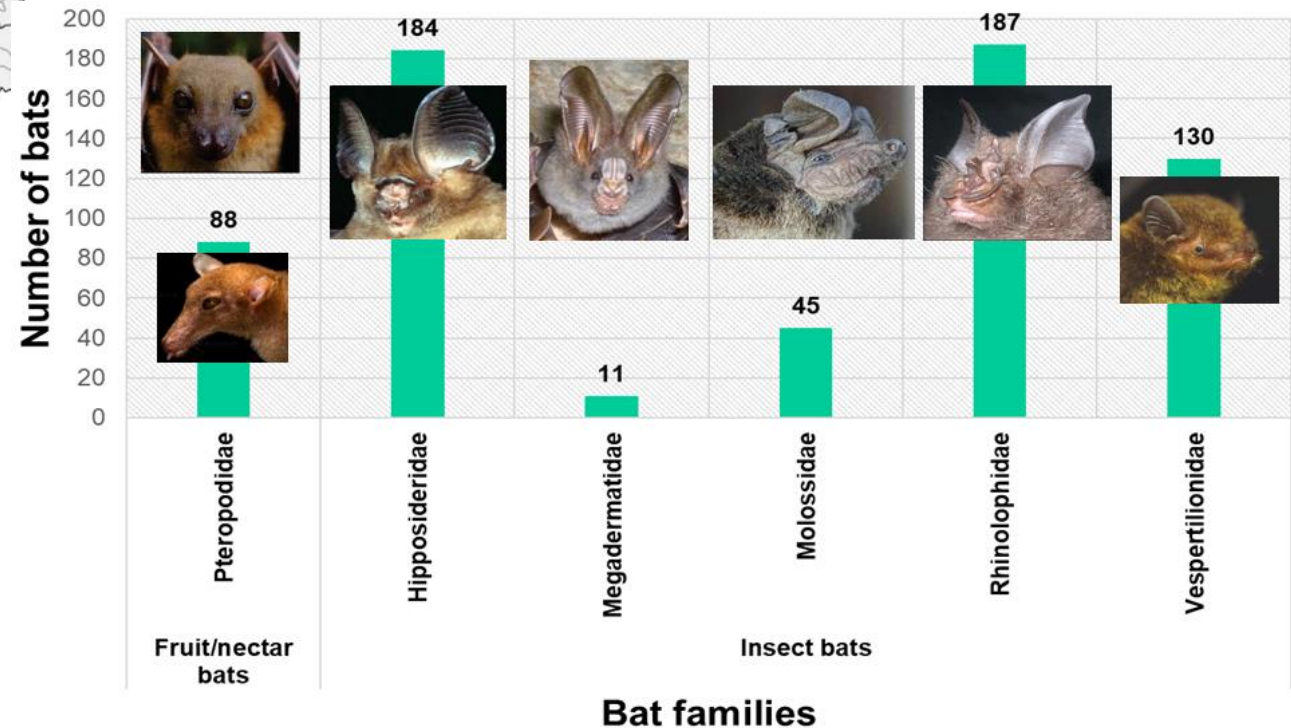
Harp trap



Mist net

- **645 bats**
  - 48 species
  - 6 families

- **Sample types**
  - Oral swabs (608)
  - Rectal swabs (539)
  - Urine (157)
  - Blood (246)





# pan-CoV screening



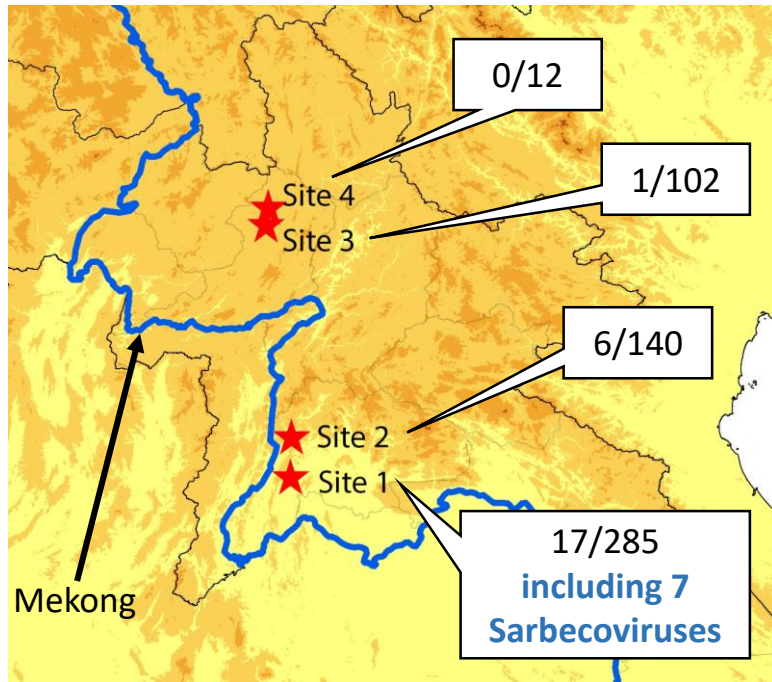
Vincent Lacoste  
IP-Laos  
(former member)

JOURNAL OF VIROLOGY, Dec. 2011, p. 12815–12820  
0022-538X/11/\$12.00 doi:10.1128/JVI.05838-11  
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## Avian Coronavirus in Wild Aquatic Birds<sup>†‡</sup>

Daniel K. W. Chu,<sup>1</sup> Connie Y. H. Leung,<sup>1</sup> Martin Gilbert,<sup>2</sup> Priscilla H. Joyner,<sup>2</sup> Erica M. Ng,<sup>1</sup>  
Tsemay M. Tse,<sup>1</sup> Yi Guan,<sup>1</sup> Joseph S. M. Peiris,<sup>1,3\*</sup> and Leo L. M. Poon<sup>1\*</sup>



N=539 rectal swabs

Anal Swab ID	Bat Genus	Bat Species	CoV Genus	CoV Subgenus	Closest sequence	% blastN similarity
BANAL-20-27	<i>Rhinolophus</i>	<i>pusillus</i>	co-infection <i>Alpha/Betacoronavirus</i>	unclassified <i>Decacovirus/Sarbecovirus</i>	Rhinolophus bat coronavirus HKU32 / SARS-CoV-2	80%
BANAL-20-51	<i>Hipposideros</i>	<i>pomona</i>	<i>Alphacoronavirus</i>	<i>Decacovirus</i>	Bat coronavirus HKU10	98%
BANAL-20-52	<i>Rhinolophus</i>	<i>Malayanus</i>	<i>Betacoronavirus</i>	<i>Sarbecovirus</i>	SARS-CoV-2	99%
BANAL-20-103	<i>Rhinolophus</i>	<i>pusillus</i>	<i>Betacoronavirus</i>	<i>Sarbecovirus</i>	SARS-CoV-2	99%
BANAL-20-115	<i>Hipposideros</i>	<i>pomona</i>	<i>Alphacoronavirus</i>	<i>Decacovirus</i>	Bat coronavirus HKU10	98%
BANAL-20-116	<i>Rhinolophus</i>	<i>malayanus</i>	<i>Betacoronavirus</i>	<i>Sarbecovirus</i>	SARS-CoV-2	98%
BANAL-20-178	<i>Hipposideros</i>	<i>pomona</i>	<i>Alphacoronavirus</i>	<i>Decacovirus</i>	Bat coronavirus HKU10	98%
BANAL-20-191	<i>Chaerephon</i>	<i>plicatus</i>	<i>Alphacoronavirus</i>	<i>Pedacovirus</i>	Porcine epidemic diarrhea virus (PEDV)	93%
BANAL-20-197	<i>Chaerephon</i>	<i>plicatus</i>	<i>Alphacoronavirus</i>	<i>Pedacovirus</i>	Porcine epidemic diarrhea virus (PEDV)	93%
BANAL-20-212	<i>Chaerephon</i>	<i>plicatus</i>	<i>Alphacoronavirus</i>	<i>Pedacovirus</i>	Porcine epidemic diarrhea virus (PEDV)	93%
BANAL-20-213	<i>Chaerephon</i>	<i>plicatus</i>	<i>Alphacoronavirus</i>	<i>Pedacovirus</i>	Porcine epidemic diarrhea virus (PEDV)	93%
BANAL-20-236	<i>Rhinolophus</i>	<i>marshalli</i>	<i>Betacoronavirus</i>	<i>Sarbecovirus</i>	SARS-CoV-2	99%
BANAL-20-242	<i>Rhinolophus</i>	<i>malayanus</i>	<i>Betacoronavirus</i>	<i>Sarbecovirus</i>	SARS-CoV-2	99%
BANAL-20-247	<i>Rhinolophus</i>	<i>malayanus</i>	<i>Betacoronavirus</i>	<i>Sarbecovirus</i>	SARS-CoV-2	99%
BANAL-20-251	<i>Hipposideros</i>	<i>khaokhouayensis</i>	<i>Alphacoronavirus</i>	<i>Decacovirus</i>	Bat coronavirus HKU10	97%
BANAL-20-273	<i>Rhinolophus</i>	<i>pusillus</i>	<i>Alphacoronavirus</i>	unclassified <i>Decacovirus</i>	Rhinolophus bat coronavirus HKU32	92%
BANAL-20-289	<i>Rhinolophus</i>	<i>affinis</i>	<i>Alphacoronavirus</i>	<i>Rhinacovirus</i>	Rhinolophus affinis bat coronavirus HKU2-related / Swine acute diarrhea syndrome related coronavirus (SADS-CoV)	98%
BANAL-20-290	<i>Eonycteris</i>	<i>spelaea</i>	<i>Betacoronavirus</i>	<i>Nobecovirus</i>	Rousettus bat coronavirus GCCDC1	99%
BANAL-20-390	<i>Eonycteris</i>	<i>spelaea</i>	<i>Betacoronavirus</i>	<i>Nobecovirus</i>	Rousettus bat coronavirus GCCDC1	97%
BANAL-20-395	<i>Eonycteris</i>	<i>spelaea</i>	<i>Betacoronavirus</i>	<i>Nobecovirus</i>	Rousettus bat coronavirus GCCDC1	99%
BANAL-20-398	<i>Eonycteris</i>	<i>spelaea</i>	<i>Betacoronavirus</i>	<i>Nobecovirus</i>	Rousettus bat coronavirus GCCDC1	99%
BANAL-20-403	<i>Eonycteris</i>	<i>spelaea</i>	<i>Betacoronavirus</i>	<i>Nobecovirus</i>	Rousettus bat coronavirus GCCDC1	99%
BANAL-20-416	<i>Cynopterus</i>	<i>sphinx</i>	<i>Betacoronavirus</i>	<i>Nobecovirus</i>	Rousettus bat coronavirus GCCDC1	99%
BANAL-20-497	<i>Myotis</i>	sp.	<i>Alphacoronavirus</i>	<i>Pedacovirus</i>	Bat alphacoronavirus*	99%

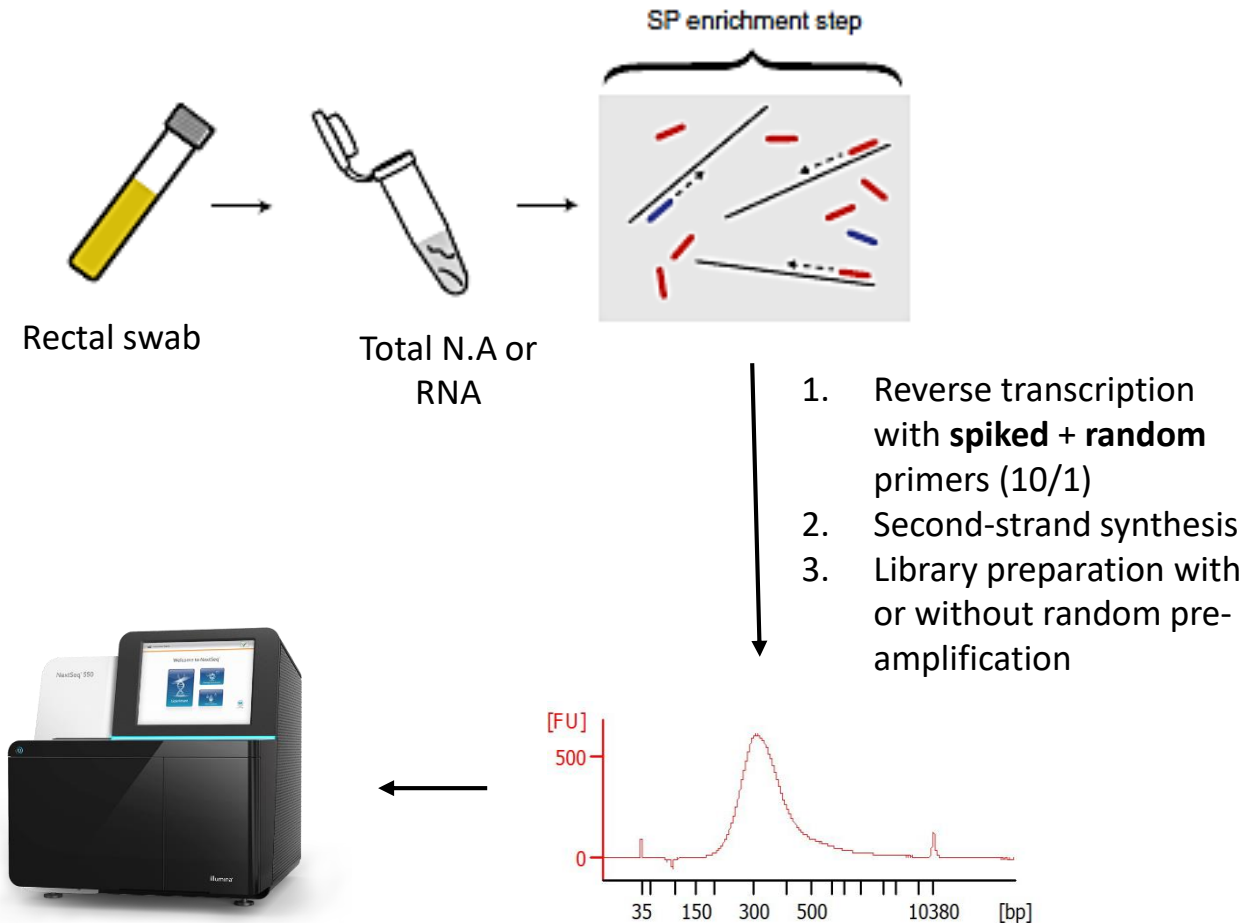
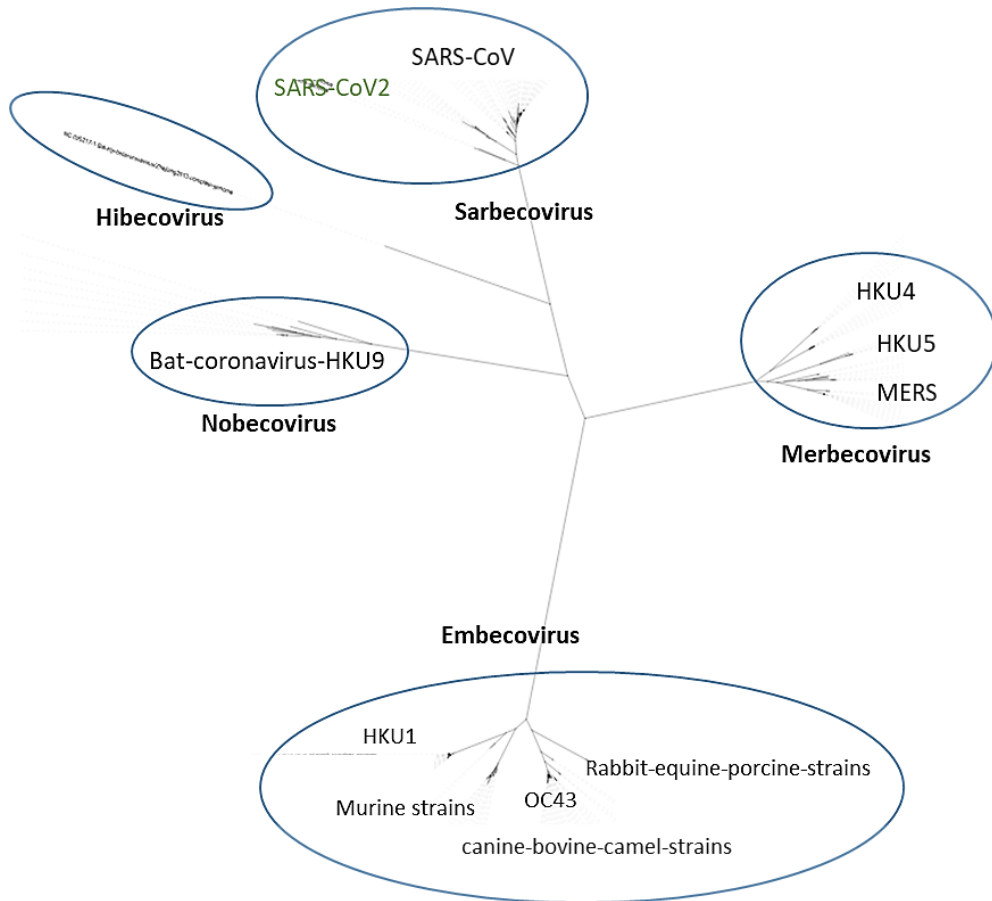


Béatrice Regnault  
IPP – Pathogen  
Discovery lab.

# Betacoronavirus enrichment

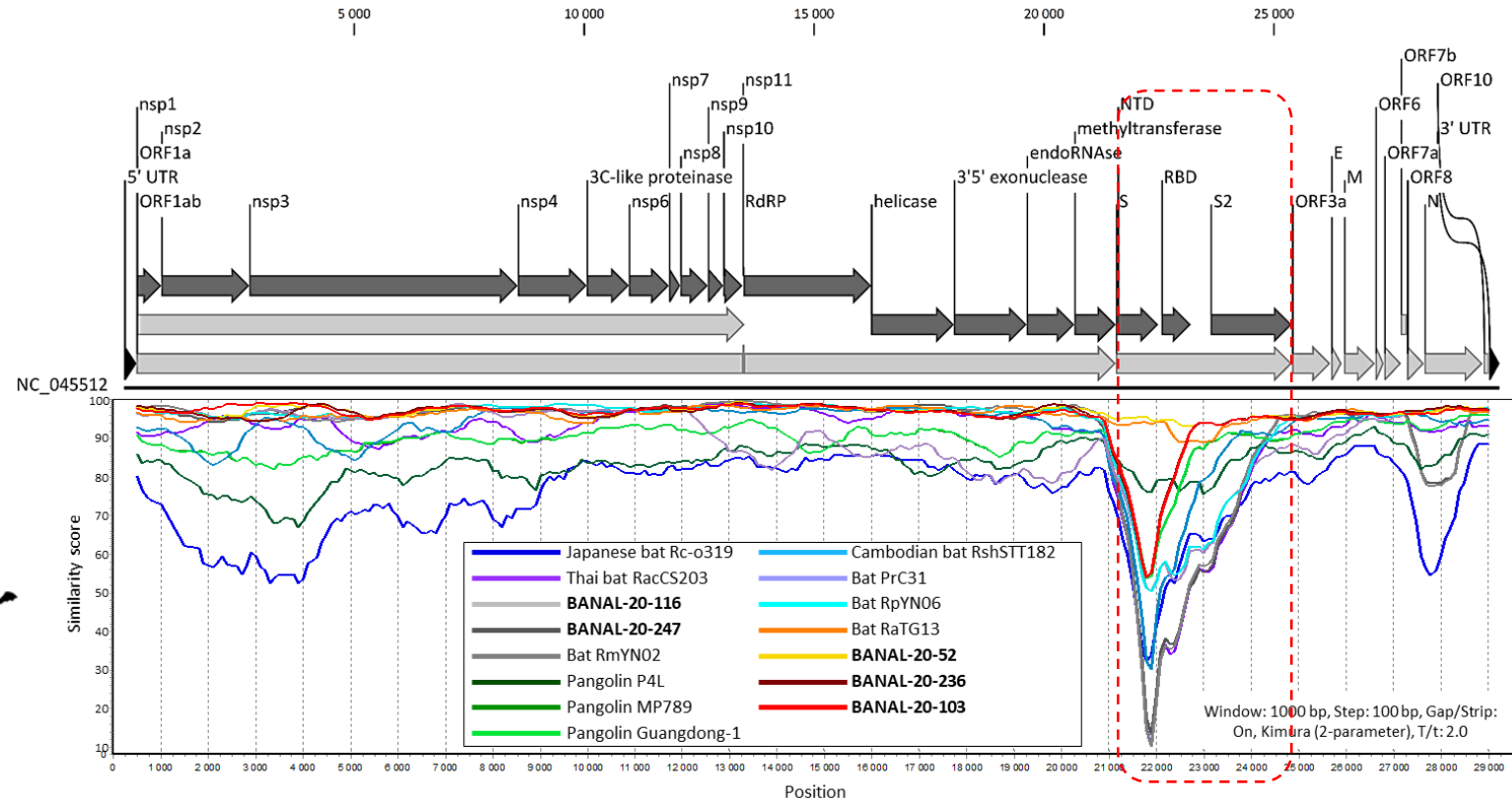
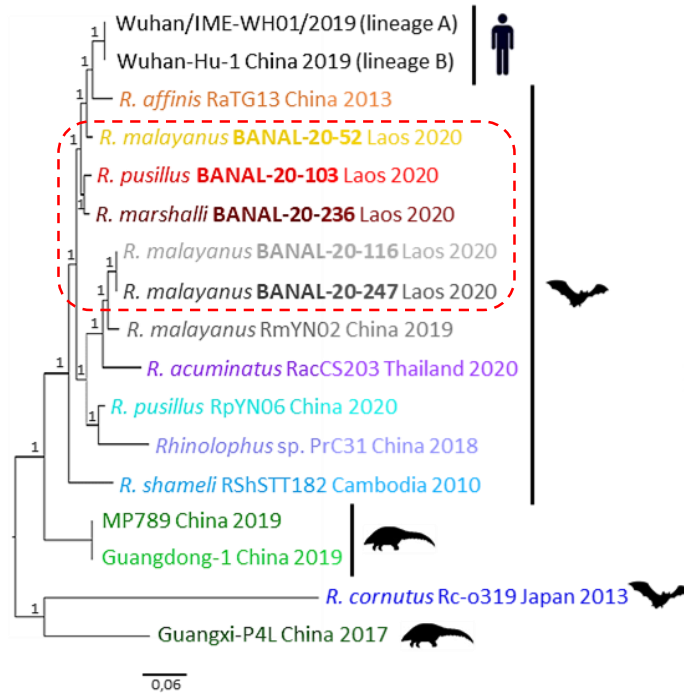
➤ **In-silico probe design** from nucleotide sequence alignment of all *Betacoronavirus* subgenera

- 13-mer primers pan-generic or specific to each subgenus (MSSPE method) Deng X. et al., 2020 Nat. Microbiol. doi: 10.1038/s41564-019-0637-9
- 432 primers





# Evolution history of bat CoVs



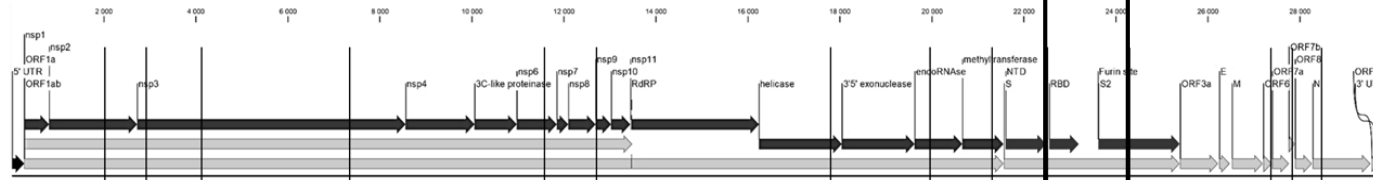
## ➤ At the whole genome level

- BANAL viruses close to SARS-CoV-2 early strains
- High degree of conservation between CoVs carried by different *Rhinolophus* species living in sympatry

## ➤ Similarity along the genome

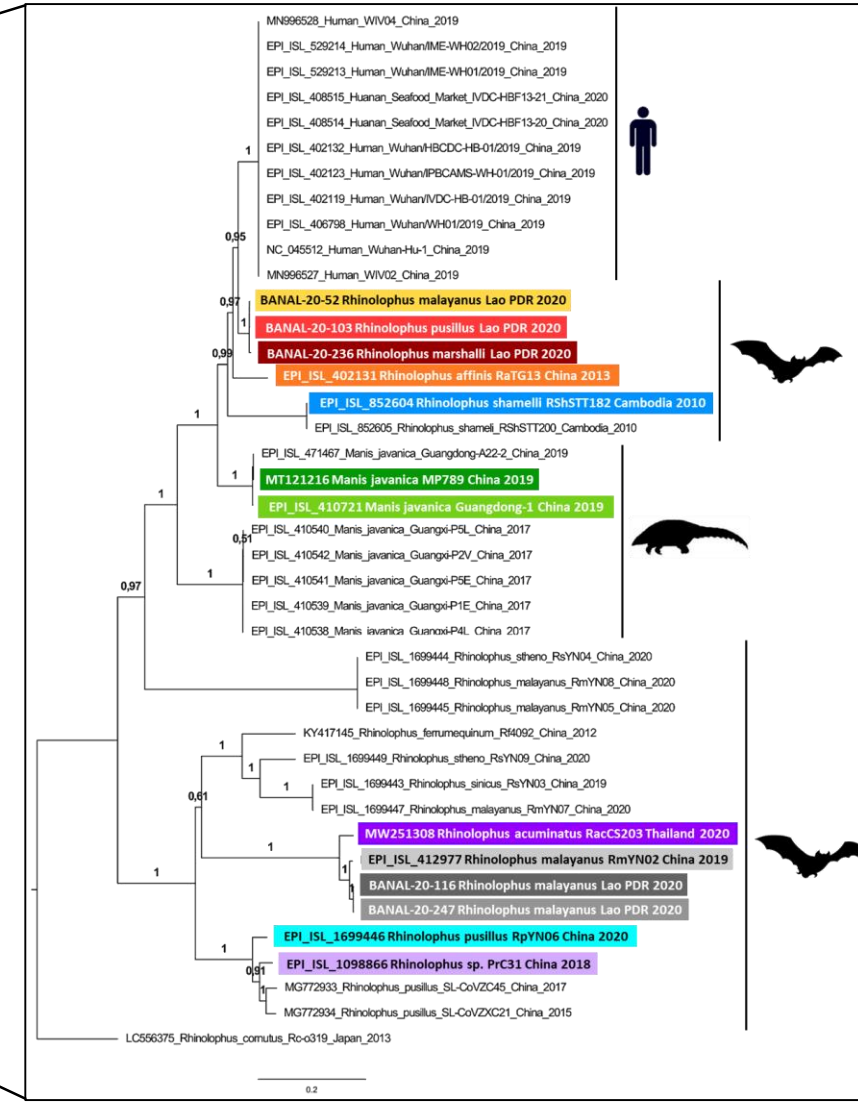
- BANAL viruses present >95% nt identity along the genome, BANAL-52 the closest known to date
- In the spike, BANAL viruses closer to SARS-CoV-2 than bat and pangolin CoVs
- No furin site

# Evolution history of bat CoVs



Fragment no:

Fragment no:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
SARS-CoV-2	RmYN02	BANAL-103	MULT	MULT	RpYN06	MULT	MULT	RmYN02	BANAL-52	RaTG13	MULT	MULT	BANAL-52	MULT	
Bat RaTG13	MULT	MULT	MULT	MULT	MULT	MULT	MULT	MULT	MULT	SARS-CoV-2	MULT	MULT	MULT	MULT	MULT
BANAL-20-52	BANAL-236		BANAL-103		MULT		BANAL-236		MULT	MULT	MULT	MULT		SARS-CoV-2	MULT
BANAL-20-103	MULT	MULT	BANAL-52		MULT	MULT	MULT	MULT	MULT	BANAL-236		MULT	MULT	MULT	MULT
BANAL-20-236	BANAL-52	RacCS-203	MULT		BANAL-247		BANAL-52		MULT	BANAL-103		MULT	MULT	MULT	MULT
Pangolin Guangdong-1							MP789				MULT		MP789		MP789
Pangolin MP789							Guangdong-1				Guangdong-A22-2		Guangdong-1		Guangdong-1
Bat PrC31	MULT		RmYN02		MULT	MULT	Rf4092		MULT	RpYN06		MULT		MULT	RpYN06
Bat RpYN06	MULT	MULT	MULT	MULT	SARS-CoV-2		RmYN02		MULT	BANAL-236	PrC31	MULT		RmYN02	PrC31
Cambodian bat RShSTT182							RShSTT200								RShSTT200
BANAL-20-116			BANAL-247				MULT			BANAL-247					BANAL-247
BANAL-20-247			BANAL-116				BANAL-236			BANAL-116					BANAL-116
Bat RmYN02	SARS-CoV-2		PrC31		MULT		RpYN06		SARS-CoV-2	MULT	MULT	MULT		RpYN06	MULT
Thai bat RacCS203	MULT	MULT	BANAL-236		MULT		MULT		MULT	MULT	MULT	MULT		MULT	MULT



## ➤ Numerous recombinations in SARS-CoV-2 history

- No pangolin CoV as direct contributor
- One / multiple ancestors depending on the fragment of genome
- In the spike: RaTG13 CoV for the NTD, BANAL CoVs for RBD and N-terminal part of S2 (including the furin site)

# Bat CoV RBD highly similar to SARS-CoV-2

SARS-CoV-2 lineage A	319	RVQPTESIVRFPNITNLCPFGVEVFNATRFASVYAWNRRKRISNCVADYSVLYNSASFSTFKCYGVSPTKLNLDLCFTNVYADSFVIRGDEVQRQIAPGQTGKIADYNYKLPDDFT	430
SARS-CoV-2 lineage B	319	RVQPTESIVRFPNITNLCPFGVEVFNATRFASVYAWNRRKRISNCVADYSVLYNSASFSTFKCYGVSPTKLNLDLCFTNVYADSFVIRGDEVQRQIAPGQTGKIADYNYKLPDDFT	430
<b>BANAL-20-52</b>	319	.....T.....T.....V.....	430
Bat RaTG13	319	.....D.....T.....T.....	430
Pangolin P4L	317	.....I.....SK.....T.....VK.....V.....	428
<b>BANAL-20-103</b>	315	.....D.....T.....T.....V.....	426
<b>BANAL-20-236</b>	315	.....D.....T.....T.....V.....	426
Pangolin Guangdong-1	315	.....T.....T.....V.....R.....	426
Pangolin MP789	315	.....T.....T.....V.....R.....	426
Bat PrC31	315	.....Q.V.....V.....HK.....P.....E.TK..D.I...T.F...T.....S..I...S...T.L.FS...V.....V.....	426
Bat RpYN06	315	.....Q.V.....V.....HN.....P.....E.TK..D.I...T.F...T.....S..I...S...T.L.FS...V.....V.....	426
Cambodian bat RShSTT182	306	..TS..TQV.....T.....R.....TT.....V.....M.....	417
<b>BANAL-20-116</b>	298	..L.STEV.....F...DK.....FN...Q.TK..D.I...T...T.....S..I...S...T.L.FS...E...V.....	409
<b>BANAL-20-247</b>	298	..L.STEV.....F...DK.....FN...Q.TK..D.I...T...T.....S..I...S...T.L.FS...E...V.....	409
Bat RmYN02	298	..IL.STEV.....F...DK.....PN...Q.TK..D.I...T...T.....S..I...S...T.L.FS...E...V.....	409
Thai bat RacCS203	298	..L.STEV.....F...DK.....PN...Q.TK..D.I...T...T.....S..I...S...T.L.FS...E...V.....	409
Japanese bat Rc-o319	293	.....QDTV.....S.....T.....R.....Q.....S.....V.....	404

SARS-CoV-2 lineage A	431	GCVIAWNSNNLDSKVGNGNYLYRFLFRKSNLKPFFERDISTEIQAGSTPCNGVEGFNCYFPLOS YGFQPTNGVGYQPYRVVVL SFELLHAPATVCGPKKSTNLVKNKCVNFN	541
SARS-CoV-2 lineage B	431	GCVIAWNSNNLDSKVGNGNYLYRFLFRKSNLKPFFERDISTEIQAGSTPCNGVEGFNCYFPLOS YGFQPTNGVGYQPYRVVVL SFELLHAPATVCGPKKSTNLVKNKCVNFN	541
<b>BANAL-20-52</b>	431	.....KHI.A.E...F.....A.....K...QT.L...Y.YR...Y.D...H.....N.....I.....	541
Bat RaTG13	431	.....KHI.A.E...F.....A.....K...QT.L...Y.YR...Y.D...H.....N.....I.....	541
Pangolin P4L	429	.....VKQ.ALT...G.....K.....QV.L...Y.ER...H..T.N...F.....NG...L.T..D.....	539
<b>BANAL-20-103</b>	427	.....H.....N.....I.....	537
<b>BANAL-20-236</b>	427	.....H.....N.....I.....	537
Pangolin Guangdong-1	427	.....H.....N.....Q.....	537
Pangolin MP789	427	.....H.....N.....Q.....	537
Bat PrC31	427	.....TAKQ.VG---S.F..SH.STK.....L.SDE-----R---T.ST.D.N.NVPLE..AT.....N.....L.Q...Q.....	518
Bat RpYN06	427	.....TAKQ.VG---S.F..SH.STK.....L.SDE-----R---T.ST.D.N.NVPLE..AT.....N.....L.Q...Q.....	518
Cambodian bat RShSTT182	418	.....IS..A--..S.Y...V.....QL...DK..S---PD.....Y..S.....N.....H..V.....	523
<b>BANAL-20-116</b>	410	..L...TAQQ.IG---S.F..SH.AVK.....L.SDE-----R---T.ST.D.N.NVPLD..AT.....N.....L.Q...R.....	501
<b>BANAL-20-247</b>	410	..L...TAQQ.IG---S.F..SH.AVK.....L.SDE-----R---T.ST.D.N.NVPLD..AT.....N.....L.Q...R.....	501
Bat RmYN02	410	..L...TAQQ.IG---S.F..SH.AVK.....L.SDE-----R---T.ST.D.N.NVPLD..AT.....N.....L.Q...R.....	501
Thai bat RacCS203	410	..L...TAQQ.IG---S.F..SH.AVK.....L.SDE-----R---T.ST.D.N.NVPLD..AT.....N.....L.Q...R.....	501
Japanese bat Rc-o319	405	..L...R.Q.ASTS..E..Y..IW.SEK.R.....AHYD..V..TQFKS---S..KN...YSSA.DSH.....N.....Q..E.I.....	506

## ➤ Alignment of the RBD region

- BANAL-52 (*R. malayanus*) closer to SARS-CoV-2 than any bat / pangolin CoVs
- 15-16/17 aa residues interacting with hACE2 receptor conserved between BANAL viruses and SARS-CoV-2 (13/17 for Cambodian bat *R. shameli* and 11/17 for Chinese bat *R. affinis* RaTG13)

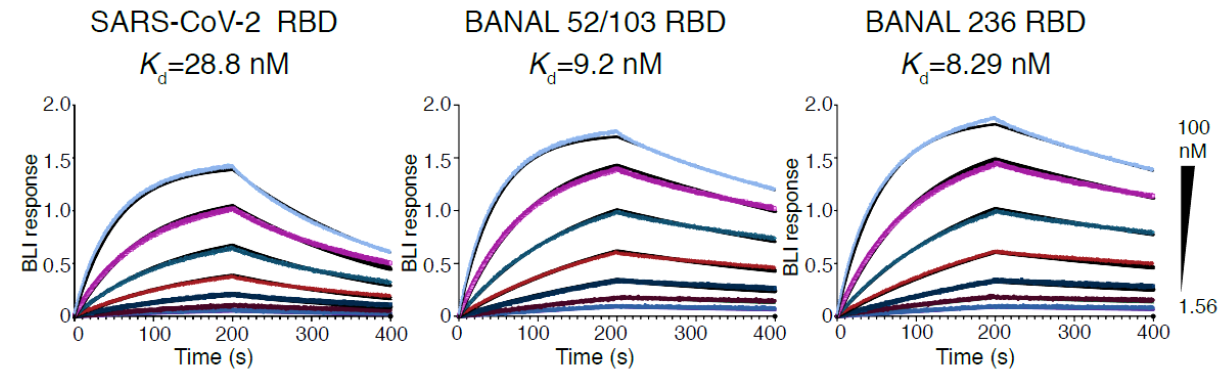
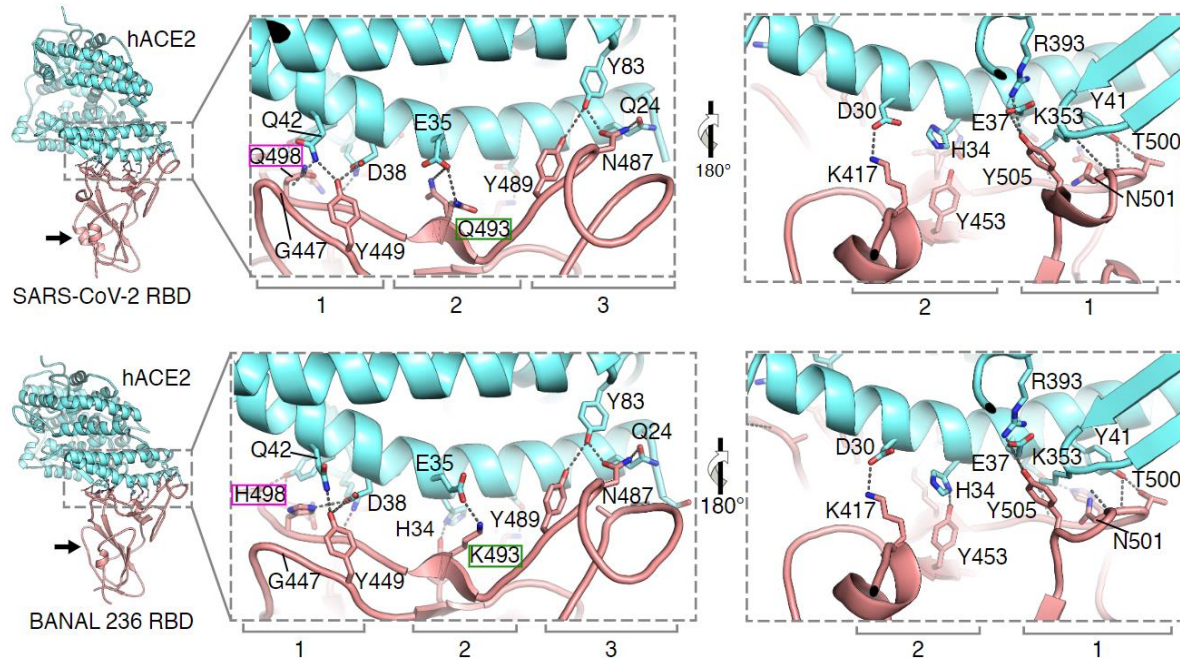


# Insights into RBD/hACE2 complex



**Eduard Baquero-Salazar**  
IPP – Structural Virology

**Massimiliano Bonomi**  
IPP – Structural Bioinformatics



## ➤ Determination of the crystal structure of BANAL RBDs

## ➤ Effects of mutations in RBD-hACE2 interactions

- BANAL mutation  $H498^Q$  disrupt transient hydrogen bonds but is known to increase affinity of SARS-CoV-2 RBD for hACE2 *Huang et al., 2021 EBioMedicine*
- BANAL mutations  $K493^Q \rightarrow$  2 additional salt bridges formed between BANAL-236 RBD & ACE2  $\rightarrow$  possible  $\nearrow$  affinity

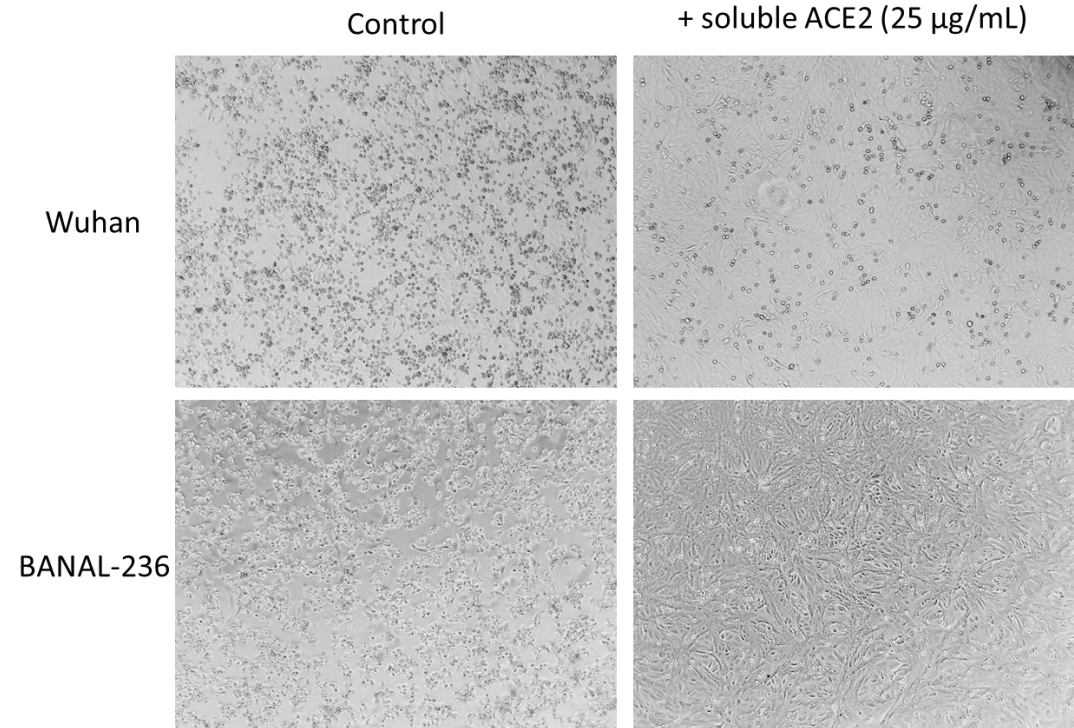
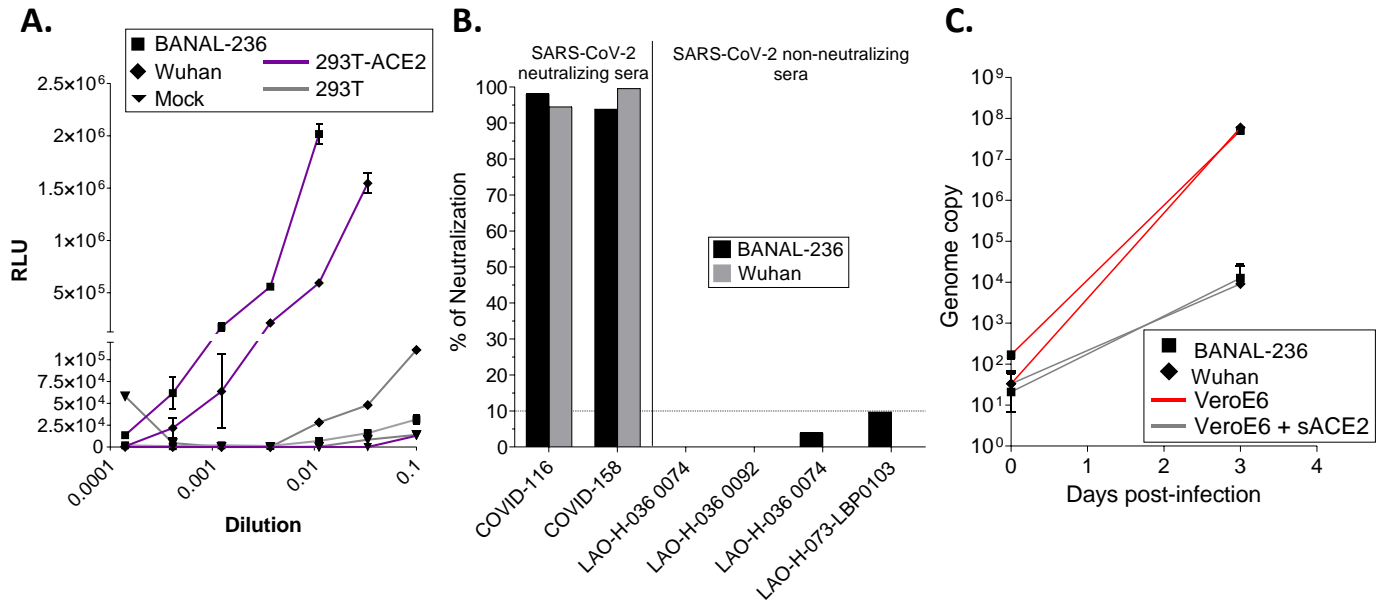
## ➤ Biolayer interferometry

- $K_d$  BANAL viruses  $\ll$  SARS-CoV-2  $\rightarrow$   $\nearrow$  affinity of BANAL viruses compared to SARS-CoV-2 Wuhan strain

# Cell entry through ACE2-dependent pathway



**Sandie Munier**  
IPP – Molecular  
Genetics of RNA  
Viruses



## ➤ Lentiviral pseudoparticles expressing Wuhan or BANAL-236 wild type spikes

- Entry in 293T cells expressing hACE2
- Entry blocked by SARS-CoV-2 neutralizing sera

## ➤ BANAL-236 virus isolation

- Infection VeroE6 expressing endogenous ACE2
- Infection blocked by soluble ACE2 (-3,6 log<sub>10</sub>) similar to Wuhan (-3,8 log<sub>10</sub>)



# Virus isolation

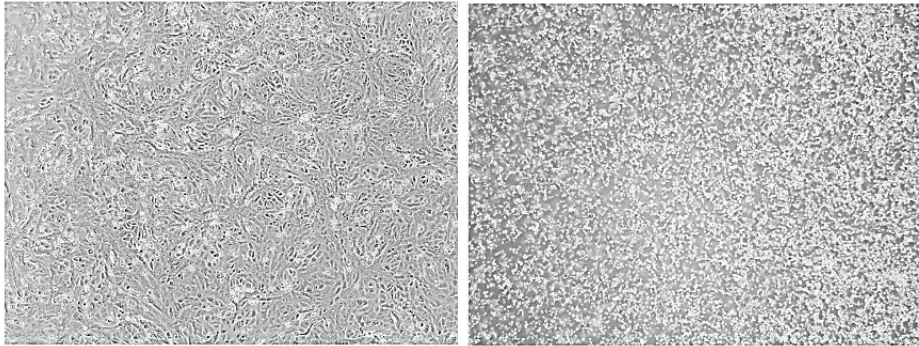


**Flora Donati**  
IPP – Molecular  
Genetics of RNA  
Viruses

**Neg control**

**BANAL-236**

VeroE6

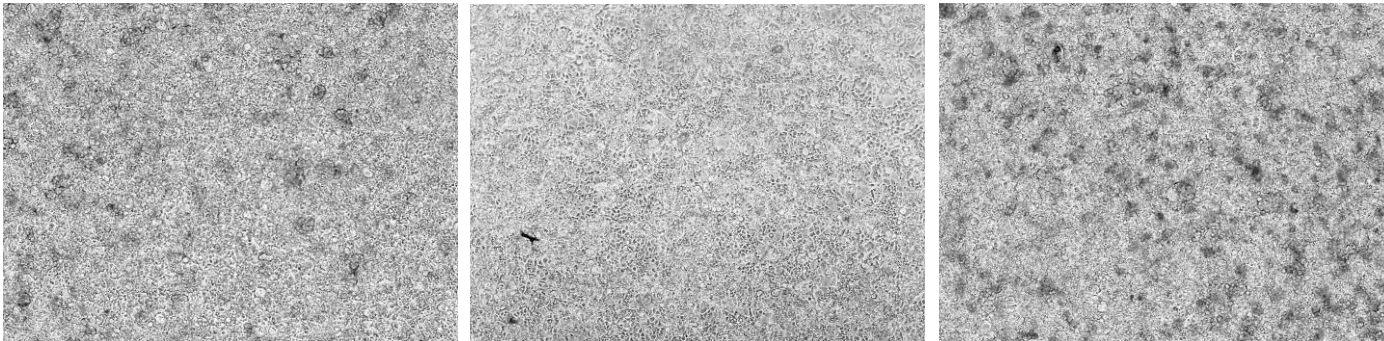


## ➤ BANAL-236 virus growth

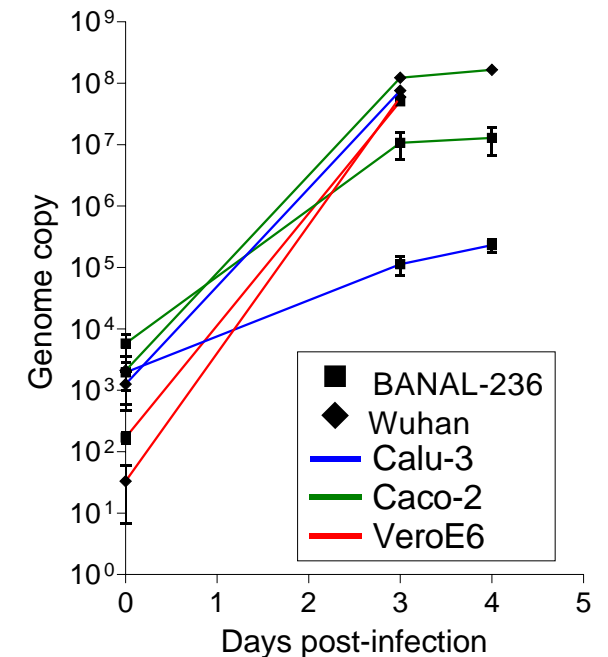
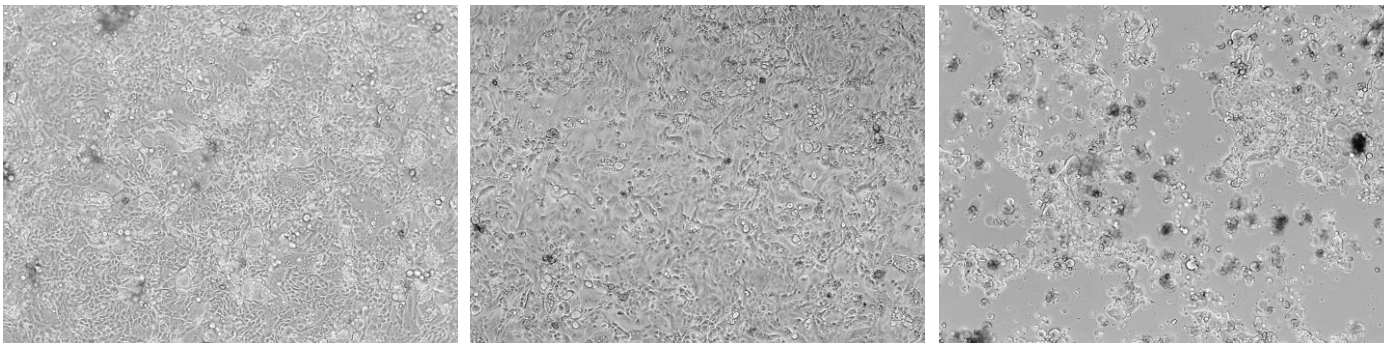
- Efficient replication in VeroE6, similar yield compared to Wuhan
- Lower replication in human cells expressing endogenous ACE2
  - No CPE observed compared to Wuhan

**Wuhan**

Caco-2

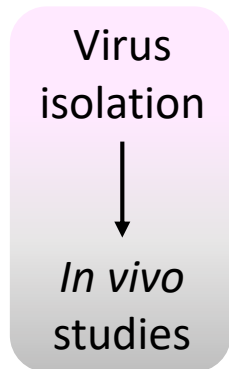


Calu-3





# Ongoing studies

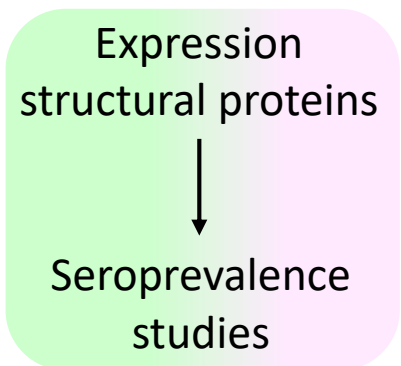


## ➤ Pathogenicity in animal model (mice + primates)

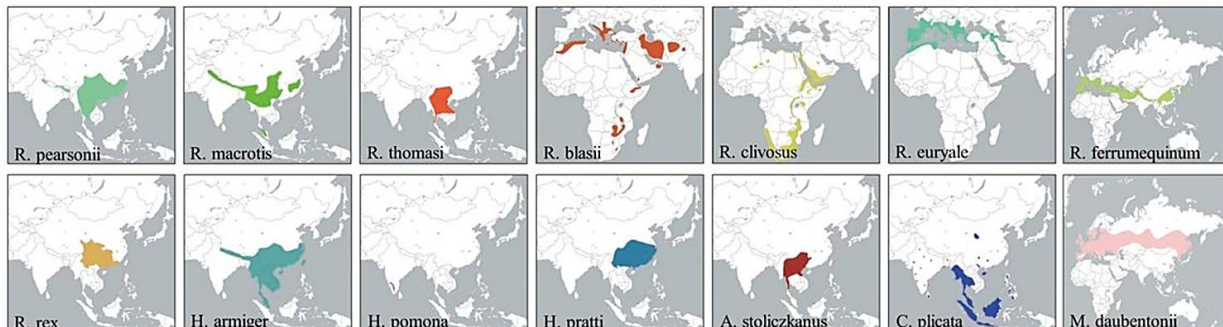
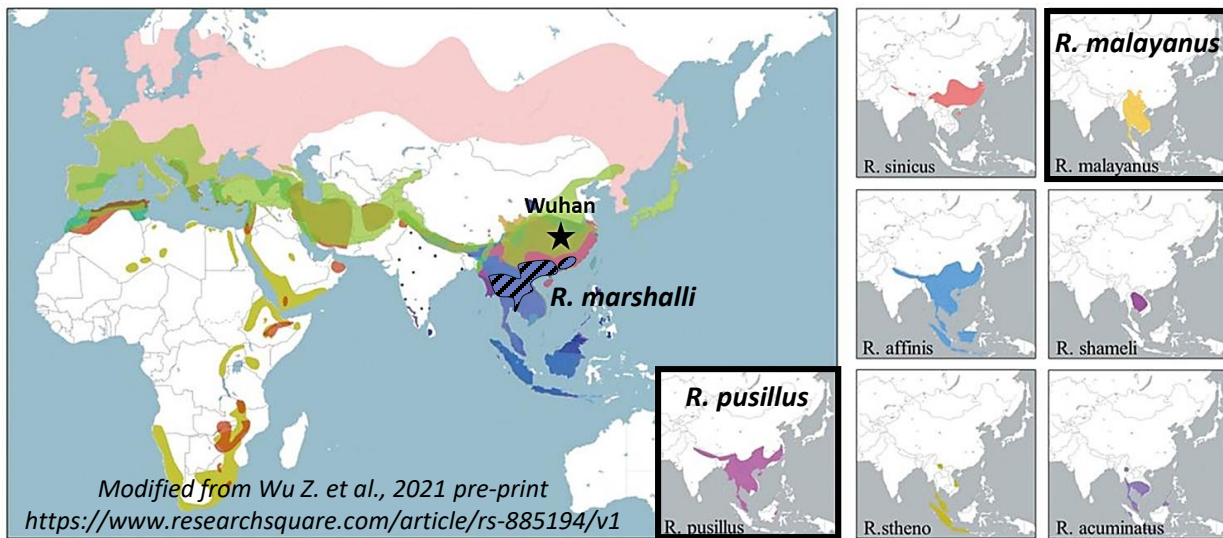
- Level of replication in classical or humanized mice
- Virus tropism in different organs
- Adaptation mutations
- Immune response to infection
- Cross-protection against SARS-CoV-2
- etc...

## ➤ Infection of Laotian populations?

- In 2020, low seroprevalence in humans Virachith et al., 2021 Lancet Reg Health West Pac.
  - Impact of governmental measures?
  - Young age population?  
or...
  - Cross-protective immunity?
- Serosurvey of general vs bat-exposed populations
  - LIPS: RBD, N, full S
  - PNT



# Conclusions



## ➤ SARS-CoV-2 origin

- **Recombination** from different *Rhinolophus* CoVs living in the limestone cave system of S-E. Asia
  - Rich diversity of bats living in sympatry → ↗ exchanges of viruses
  - Major route of transmission: feces (but oral swabs also >0 for BANAL-27)
- **No need for an intermediate host** to increase affinity for ACE2, but...
  - Origin of the furin cleavage site?
- **Route of introduction** to the human population?

## ➤ Risk of emergence of other bat CoVs?

- **Exposure** of guano collectors, religious communities, tourists?
- If yes, **symptomatic** infection? Cross-protection against SARS-CoV-2?

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