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Probing the reliability of DNA barcodes in delineating geographically widespread bird species

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Studies on birds have shown the efficiency of cytochrome *c* oxidase subunit I (COI) barcodes to identify and assign more than 95% of the species to their respective families. These studies indicate that small, inconspicuous birds are good candidates as cryptic species or show allopatric divergences, whereas the larger birds which can fly/swim long distances show lesser divergences. Here we attempt to check the efficiency of COI barcodes in delineating species with worldwide distribution. We analyse genetic differences in birds of the family Ardeidae with global distribution to evaluate the possibility of allopatry. COI barcodes and sequences of a variable region of cytochrome *b* gene were compared in seven out of nine widely distributed Ardeidae species and we found deep intra-specific divergences and diagnostic mutations in four species. Whether these sequence divergences are evolutionarily significant needs to be further analysed.

Keywords: Birds, DNA barcodes, cytochrome *c* oxidase subunit I, cytochrome *b*.

A DNA barcode system envisages a library based on the sequence diversity in a standard region of the mitochondrial cytochrome *c* oxidase subunit I (COI) to accurately identify all animal species and to speed up the discovery of new species[1]. Extensive studies on birds have shown the efficiency of the barcodes in correctly identifying and assigning more than 95% of the species studied to their respective families[2–5]. Some of these earlier studies have also shown that a standard threshold of 10 × mean intra-specific variation in the COI sequences can correctly assign individuals in more than 90% of the species. Further, Tavares and Baker[6] showed that mitochondrial DNA barcodes are extremely effective in identifying closely related sister species in well-studied groups like birds. All sister-pairs were characterized by reciprocally monophyletic lineages and species which comprised of several divergent monophyletic lineages could be flagged as new unrecognized species. Such species could be further

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checked with multiple gene sequences to counter any biases in species detection. Based on these studies, we are now in the process of developing a comprehensive database of partial sequences of COI and cytochrome *b* (cyt *b*) genes, of resident and migratory birds of India. Preliminary survey of close to 300 species showed that individuals could be correctly assigned to their species in most of the cases without any ambiguities.

Generally, similarities in external appearances and lifestyles between the New World and Old World bird species, or birds with worldwide distribution have been interpreted to reflect a close phylogenetic relationship. The same is also reflected in previous studies on bird barcoding done extensively in the Nearctic and the Neotropics with a smattering of work done in other regions. Kerr *et al.*[7] barcoded 500 species of Argentinian birds and compared the patterns of sequence divergences in these birds with those in North America. In this study, out of the 42 species whose breeding range extends from Argentina to North America, 32 species showed divergences less than the standard 10× threshold. These mainly included waterbirds and raptors whose coastal habitats and long-distance movements facilitate gene flow. The remaining 10 species showed deeper genetic divergences and were mostly plain-coloured passerines and birds with cryptic lifestyles and disjunct ranges. Prior studies on the North American bird species also revealed 15 species with deep intraspecific divergences and most of these species are small to medium-sized, plain-coloured birds[2,4]. Johnsen *et al.*[5] compared sequence divergences among 78 Holarctic species occurring both in Scandinavia and North America and reported 19 species with deep genetic divergences. A majority of these species are inland breeding birds. Therefore, studies so far indicate that small, inconspicuous birds with limited ranges are good candidates for unrecognized species or show allopatric divergences, whereas the larger birds which can fly/swim long distances show lesser divergences due to a strong gene flow.

But immense geographical barriers, like the oceans separating the New World and the Old World, are known to impede genetic exchange even in the common migratory species of birds with global distribution. In such cases we can naturally expect allopatric divergences, even when the separated populations have co-evolved over time in such a way that they have the same morphology and behaviour. But can the genetic differences in such species be highlighted by barcoding? To answer this question we analysed samples of some common species of the family Ardeidae (herons) with worldwide distribution.

The family Ardeidae (order Ciconiiformes) includes 12 genera and 19 species in India. Out of the 19 species found in India, 9 are distributed widely across the world. In this communication, we compare the divergence patterns in the barcode region of the COI gene and a variable region of the cyt *b* gene[8] in samples from seven of these nine species collected from diverse locations in India with those available from the rest of the world in the NCBI database, with a view towards understanding mitochondrial genetic variations in the New World and Old World birds. The aim of this study is to verify the robustness of COI barcodes and cyt *b* sequences in clearly highlighting the differences in common species with worldwide distribution.

The specimen for this study included seven of nine widely distributed species, representing four of the seven genera of the family Ardeidae. We followed Salim Ali[9] and Clements' systematic assignment[10] in classifying all avian species. Fresh feathers were collected from live birds housed at various Zoological Parks in India and stored at room temperature in sterile envelopes. Blood was collected in EDTA from the brachial artery and stored at –20°C. Tissue samples (muscle, bone) from dead birds found in various nesting locations in Andhra Pradesh and Gujarat were collected in absolute alcohol and frozen at –70°C. In case of blood or fresh feathers, the birds were photographed prior to release. Genomic DNA was extracted from these samples using the phenol–chloroform method[11].

To evaluate the genetic relationships within and between species of the family Ardeidae, partial sequences of the mitochondrial cyt *b* and COI genes, which can provide information on phylogeny in delineating species were amplified. Universal primers, mcbF (5′-TACCATGAGGACAAATATCATTCTG-3′) and mcbR (5′-CCTCCTAGTTTGTTAGGGATTGATCG-3′) were used to generate a 440 bp amplicon of the cyt *b* gene[8] and about 660 bp sequence of the COI gene was amplified using BirdF1 (5′-TTCTCCAACCACAAAGACATTGGCAC-3′) and BirdR1 (5′-ACGTGGGAGATAATTCCAAATCCTG-3′)[2]. In the absence of amplifications, an alternate reverse primer BirdR2 (5′-ACTACATGTGAGATGATTCCGAATCCAG-3′) was used. In addition to the above-mentioned primers, LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) were employed to amplify the Folmer region of the COI gene[12]. PCR products were obtained following standard protocols described in the respective papers[8,2,12]. The products were visualized on 1.5–2% agarose gels depending on the amplicon size. Amplicons were cleaned using QIA quick columns (Qiagen Inc) and both strands were sequenced on an ABI 3730 DNA Analyzer.

The resultant contigs were assembled using Codoncode Aligner 3.01 and individual genes were aligned in Clustal X[13] with parameters set to default. Phylogenetic tree was constructed using neighbour-joining (NJ) analysis under K2P model with 1000 replications for both cyt *b* and COI genes[14]. Sequence divergence, node bootstrap values and pairwise mean distances were calculated[15] among haplotypes of each dataset in MEGA 4.1. Based on the NJ analyses and sequence divergence data, we

Table 1. COI and cyt *b* sequences retrieved from the database of birds of the family Ardeidae

Species	mtDNA genes	Accession no.	Location
Large egret (*Ardea alba*)	COI	EF515753	South Korea
		DQ433327-28	Surinam; South America
		DQ432747	Florida, USA
	cyt *b*	AF193822	Louisiana, USA
Grey heron (*Ardea cinerea*)	COI	EF515755	South Korea
		FJ808628	Korea
		GQ481372	Canada
Great blue heron (*Ardea herodias*)	COI	DQ432748	Delaware, USA
		DQ433329	Ontario, Canada
		DQ434302	Ontario, Canada
		AY666320	Ontario, Canada
	cyt *b*	AF193821	Louisiana, USA
Cocoi heron (*Ardea cocoi*)	COI	FJ027163-64	Canada
Night heron (*Nycticorax nycticorax*)	COI	AY666336	Ontario, Canada
		FJ027914	Ontario, Canada
		EF515757	South Korea
	cyt *b*	AF193829	Baton Rouge, USA
Median egret (*Mesophoyx intermedia*)	COI	EF515756	Korea
Cattle egret (*Bubulcus ibis*)	COI	FJ027232-34	Canada
		DQ433383-84	Canada
		DQ432776	Canada
	cyt *b*	DQ485898	USA

Table 2. Specimen details, fixed mutations (cyt *b* and COI genes) and mean distances (COI) for four congeneric pairs of species belonging to the family Ardeidae

		No. of individuals		Fixed mutations		
Species	Sample code	cyt *b*	COI	cyt *b* (442 bp)	COI (666 bp)	Mean distance (COI) (%)
A. alba	a. *A. alba* (OW)	2	8	a versus b = 27	a versus b = 31	a versus b = 2.4
	b. *A. alba* (NW)	1	3			
A. cinerea	a. *A. cinerea* (OW)	5	6		a versus b = 11	
	b. *A. herodias* (NW)	1	4	a versus b = 13	b versus c = 05	a versus b versus c = 1.1
	c. *A. cocci* (NW)	–	2		c versus a = 10	
N. nycticorax	a. *N. nycticorax* (OW)	3	4	a versus b = 19	a versus b = 19	a versus b = 1.8
	b. *N. nycticorax* (NW)	1	2			
B. ibis	a. *B. ibis* (OW)	5	3	a versus b = 10	a versus b = 09	a versus b = 0.8
	b. *B. ibis* (NW)	1	6			

determined the clusters which could be considered as unique species. All new sequences were deposited in GenBank with accession numbers HM804863-64, HM804869, HM804871-73, HM804875-84, HM804898-99, HM804900-05, HM804907, HM804908, HM804911-13, HM804915-18, HM804921-24 and HM804926. Additional mtDNA sequences of cyt *b* and COI were retrieved from GenBank for analysis (Table 1). Bayesian MCMC analysis was performed using MRBAYES 3.2 with four simultaneous MCMC chains, temp = 0.2 and burn-in = 0.25 for 100,000 generations to compute a consensus phylogenetic tree[16].

We used standard sets of primers to successfully amplify and sequence approximately 660 bp of COI and 440 bp of cyt *b* target regions of mtDNA. In the resultant binary tree constructed with COI sequences (Figure 1), the Old World bird, *Ardea cinerea* (Grey heron) forms a separate clade from related birds of the New World, i.e. *Ardea herodias* (Great blue heron, North America) and *Ardea cocoi* (Cocoi heron, South America). This clearly highlights that these are three different but closely related species, and the result is concurrent with the existing taxonomic classification. But *Ardea alba* (Large egret), which taxonomists have classified as a single bird species across the world, forms two distinct clusters with high bootstrap value (>99%) indicating deep COI divergence. Similarly, in other two species, *Nycticorax nycticorax* (Night heron) and *Bubulcus ibis* (Cattle egret), deep COI divergences between the Old World and New World birds are highlighted. Similar analysis of the cyt *b* data for

these four congeneric pairs of species recovered compatible pattern variations as those highlighted in the COI tree (Figure 2). Additionally, we obtained similar topologies with COI barcodes generated for these four congeneric pairs of species, i.e. *A. alba*, *A. cinerea*, *B. ibis* and *N. nycticorax* using MRBAYES (Figure 3). To eliminate the possibility of co-amplifying pseudogenes (numts), we also checked for fixed mutations and pairwise intraspecific K2P distances between different clusters of the same species (Table 2).

In 442 bp of the cyt *b* gene, we could identify 27 fixed mutations between New World and Old World individuals of *A. alba*, 13 in *A. cinerea*, 19 in *N. nycticorax* and 10 in *B. ibis*, and in approximately 660 bp of the COI, we could get 31 fixed mutations in *A. alba*, 5–11 in *A. cinerea*–*A. herodias*–*A. cocoi*, 19 in *N. nycticorax* and 9 in *B. ibis* respectively.

Intraspecific distances in *A. cinerea*, *A. herodias* and *A. cocoi* range from 0% to 0.1%. However this distance increases to 1.1% when all individuals are grouped together and analysed as members of one species, considering that they all look morphologically similar. This finding reaffirms the 10 × threshold described by Hebert *et al.*[2]. Three other species, *A. alba*, *N. nycticorax* and *B. ibis* show high intraspecific variation (0.8–2.4%) when sequences from across the world are analysed together. Here again these intraspecific variations range between 0% and 0.5% when the New World and the Old World individuals are analysed separately (Figure 4).

The effectiveness of COI barcodes in delineating and identifying species has been efficiently demonstrated in several previous studies, more so in the birds[2–5]. Hebert *et al.*[2] suggested a threshold of ten times (10 ×) the intraspecific variation to screen for splits in species. This criterion for identifying putative species has been criticized[17], and subsequent studies have conceded that the 10 × as well as the 2.7% thresholds cannot be used to flag potential new species of birds, especially in the closely related or recently evolved sister species[6]. They suggested characteristic NJ-clustering and diagnostic fixed substitutions as additional evidences to correctly assign unknown individuals or highlight potentially new species. Other mitochondrial markers, like the cyt *b*, have been used in

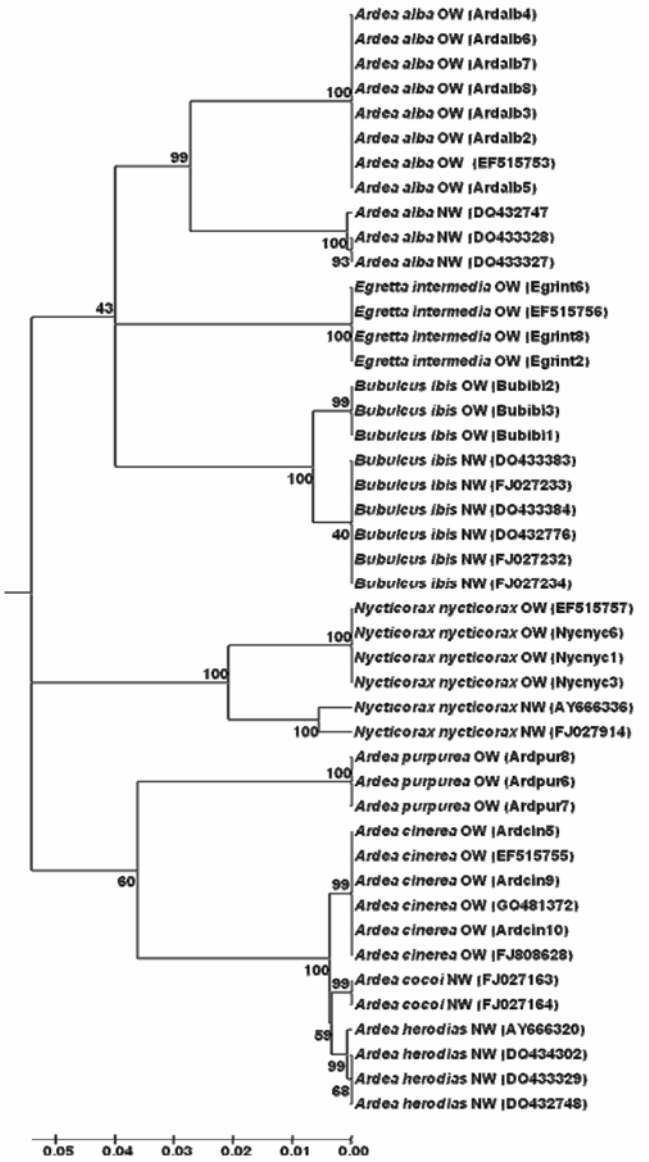

Figure 1. Neighbour-joining tree of COI barcodes of the family Ardeidae constructed with K2P genetic distances using MEGA 4.1.

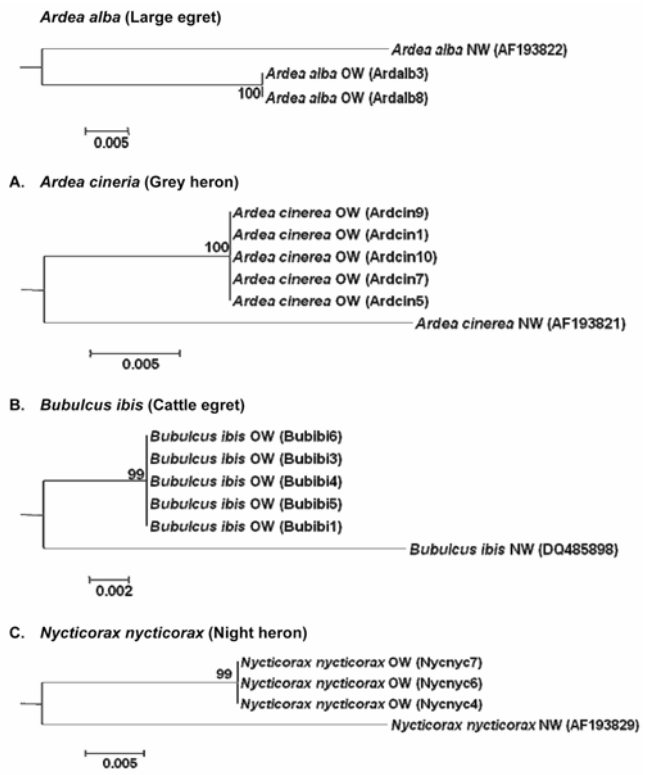

Figure 2. Neighbour-joining tree of mitochondrial cytochrome *b* sequences of the family Ardeidae constructed with K2P genetic distances using MEGA 4.1.

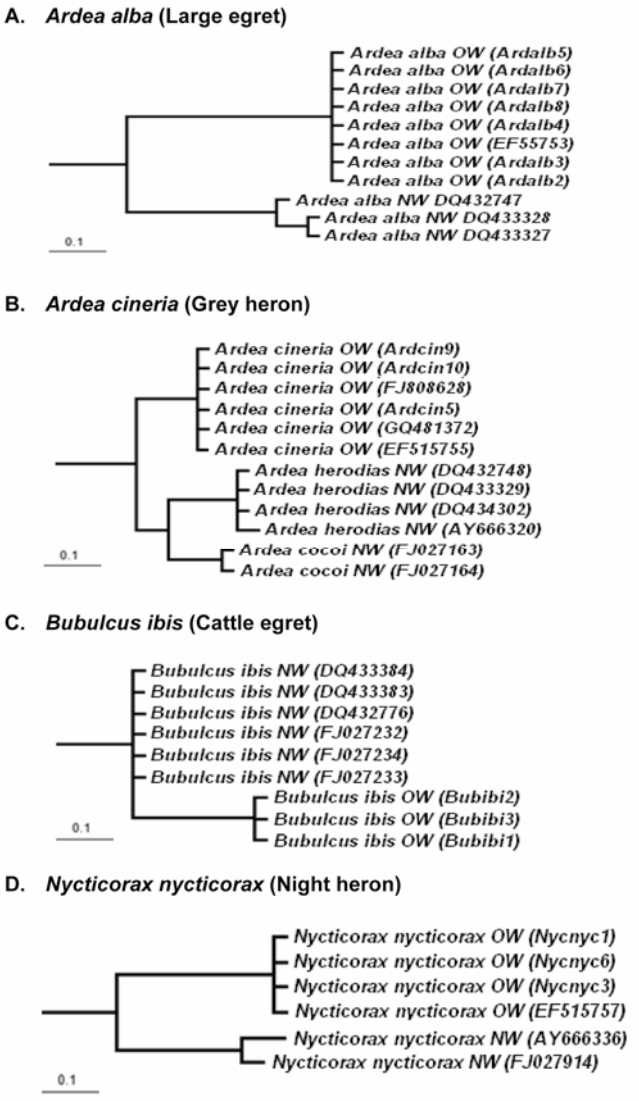

Figure 3. Bayesian topologies recovered with COI barcodes of Old World (OW) and New World (NW) birds of the family Ardeidae.

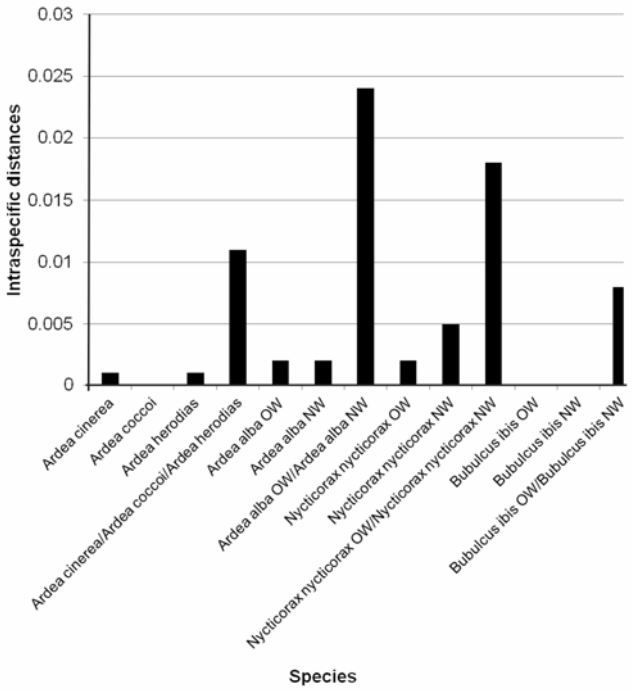

Figure 4. Graphical representation showing levels of mean intraspecific distances for four congeneric pairs of species with COI sequences.

phylogenetic studies and to complement COI in DNA barcoding[18–20]. In our study we used all the criteria recommended for identifying new species through barcoding and also analysed a variable region of the cyt *b* gene used for species identification[8].

A. cinerea is widely distributed across Asia, Africa and Europe, while an almost similar looking species, *A. herodias* is found in North and Central America, and *A. cocoi* in various parts of South America. COI barcodes of these three species confirm to the 10× cut-off and show distinct NJ-clustering, although the number of diagnostic fixed mutations is marginally lower (Table 2) than the number recommended (>12)[6]. Another species in the family Ardeidae, *B. ibis* has been earlier reported to have two distinct geographical races[21,22]. The Eastern Cattle egret, *B. ibis coromandus* breeds in Asia and Australasia, whereas the Western form, *B. ibis ibis* occupies the rest of the species range, including the Americas. COI and cyt *b* analyses of the available datasets indicate the possibility of these two geographically distinct races being recently evolved sister species (Figures 1 and 2; Table 2). In view of the results in the above described species, two other species in the family Ardeidae with worldwide distribution can be easily flagged as composite species consisting of two distinct sister species each. The Night heron (*Nycticorax nycticorax*) is widely distributed across Asia, Africa, Europe and North America. COI barcodes of samples collected in India were analysed along with sequences retrieved from the NCBI database. Distinct clades in the NJ-tree, 10× threshold and 19 fixed substitutions were seen in both the COI and cyt *b* sequences between birds of the Old World and the New World (Figures 1 and 2; Table 2). Similar results were also obtained in *A. alba*, but with the largest number of fixed mutations; 27 in the cyt *b* and 31 in the COI region. Although *A. alba* has been taxonomically classified into different geographical races, there are no reports of this species being a composite of distinct sister species. However, this species shows deeper intraspecific divergence than the sequence differences among *A. cinerea*, *A. herodias* and *A. cocoi*, and therefore can be flagged as potentially distinct sister species. When sequences of these birds from across the world were compositely analysed, the intraspecific sequence divergence was considerably higher than when the Old World and New World samples were analysed separately (Figure 4). Although large, this magnitude of intraspecific divergence did not

exceed the 2.7% threshold recommended by Hebert *et al.*[2], even for the *A. cinerea–A. herodias–A. cocoi* complex. The aim of this study is not the phylogeography of birds of the family Ardeidae, but to verify the robustness of mitochondrial markers in delineating species with worldwide distribution. Whether these sequence divergences are evolutionarily significant needs to be further analysed on a larger sample set taking into consideration more stringent criteria. Although our results are preliminary and based on few samples and sequences available in the database, they justify the need for further investigation into these species with extensive geographical sampling.

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Erratum

Terrain response to the 1819 Allah Bund earthquake in western Great Rann of Kachchh, Gujarat, India

M. G. Thakkar, Mamata Ngangom, P. S. Thakker and N. Juyal

[*Curr. Sci.*, 2012, **103**, 208–212] – In Figure 5 the 'Food wall' should be read as 'Foot wall'. The corrected figure is printed below.

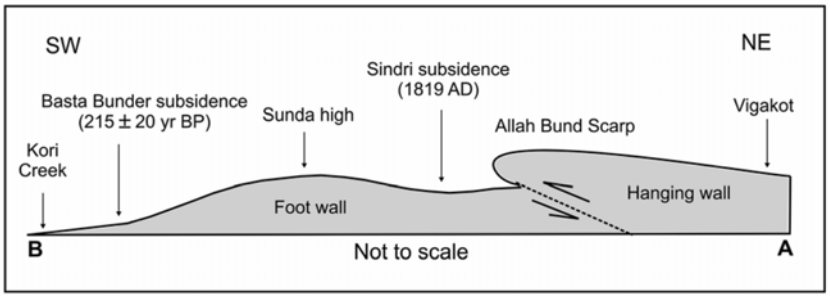

Figure 5. Schematic diagram of a cross-section from Allah Bund to Kori Creek (points A to B in Figure 1) showing a major coseismic uplift of Allah Bund accompanied by subsidiary buckling of Sindri depression and Basta Bundar subsidence separated by the Sunda uplift.