

Sequence Note

HIV Type 1 CRF13_cpx Revisited: Identification of a New Sequence from Cameroon and Signal for Subsubtype J2

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ABSTRACT

A nearly full-length genome sequence of an HIV-1 isolate originating from Cameroon, 02CM.3226MN, was found to cluster together with previously reported CRF13 sequences 96CM-4164 and 96CM-1849. Similarity plotting, bootscanning, breakpoint analysis, and phylogenetic trees confirmed similar genomic structures with almost identical breakpoint positions among these three isolates. Thus, CRF13 now fulfills the HIV-1 nomenclature requirements. A χ^2 analysis across all three genomes simultaneously was applied to more accurately determine breakpoints and address the uncertainty in such estimates. Some fragments were found to be difficult to classify, as indicated by a low branching index (BI), due to limited knowledge about parental and reference subtype sequences. One fragment with low BI association to reference subtype J sequences (BI = 0.27, cut-off for subtype classification >0.55) was found to be closer to J fragments of CRF11 similar to the way that A1–A2 and F1–F2 subsubtypes associate. This suggests that subtype J may need to be reclassified into subsubtypes J1 and J2. The CRF13 genome consists of fragments from subtypes A1, G, and both J1 and J2 as well as CRF01 and one region that was left unclassified.

INTERSUBTYPE RECOMBINATION IS AN IMPORTANT MECHANISM driving the rapid evolution of HIV-1 and it plays a major role in global and regional HIV epidemics. According to the Los Alamos HIV database, more than 20 circulating recombinant forms (CRFs) are currently recognized or have been proposed (<http://hiv-web.lanl.gov/CRFs/CRFs.html>), although not all sequence data are presently published and available.^{1,2} The majority of the CRFs have been identified in geographic regions where multiple HIV-1 subtypes cocirculate. In Cameroon, where various HIV-1 subtypes of group M, O, and N coexist, CRF01_AE, CRF02_AG, CRF11_cpx, and CRF13_cpx have been found.^{1,3–5} We have identified a third CRF13_cpx isolate (02CM.3226MN), and thus the general nomenclature requirements for defining CRFs have been met.

02CM.3226MN was sampled from a healthy, married female in Manyamen, Cameroon, who, in terms of transmission, had

no high-risk behaviors. 02CM.3226MN displayed the same genetic organization as two previously reported CRF13 isolates (96CM-4164, GenBank accession number AF460974, and 96CM-1849, GenBank accession number AF460972).⁶ The two previous CRF13_cpx sequences were reanalyzed together with 02CM.3226MN in all analyses described. The GenBank accession number for 02CM.3226MN is AY371154.

A neighbor-joining tree using F84 model distances was used to investigate overall sequence similarities between 02CM.3226MN and previously reported full-length nonrecombinant and recombinant genomes in the year 2001 HIV-1 full-length reference strains of M-group subtypes and CRFs (http://www.hiv.lanl.gov/content/hiv-db/SUBTYPE_REF/align.html). PHYLIP programs DNADIST and NEIGHBOR were used for tree reconstruction and the reliability of the constructed phylogenetic trees was assessed by nonparametric

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bootstrap from 500 alignment replicates with the PHYLIP programs SEQBOOT, DNADIST, NEIGHBOR, and CONSENSE.⁷ The obtained trees were visualized using TREEVIEW.⁸ The previously described CRF13 sequences 96CM-1849, 96CM-4164, together with 02CM.3226MN formed a separate cluster with a 99.8% bootstrap value and did not associate with any specific subtype or other recombinant virus. This suggested that this new sequence, 02CM.3226MN, had unique sequence similarities shared with CRF13_cpx.

Tree analysis including recombinant sequences is, however, problematic. While it may display overall similarities, it does not reveal any details about the recombinatory nature of the sequences and it may also confuse the tree-building method. To overcome these problems, we reanalyzed all three sequences in the new CRF13 cluster using methods that specifically investigate HIV recombination, including similarity plotting and bootscanning, an expanded version of the breakpoint analysis by a χ^2 test of informative sites, the

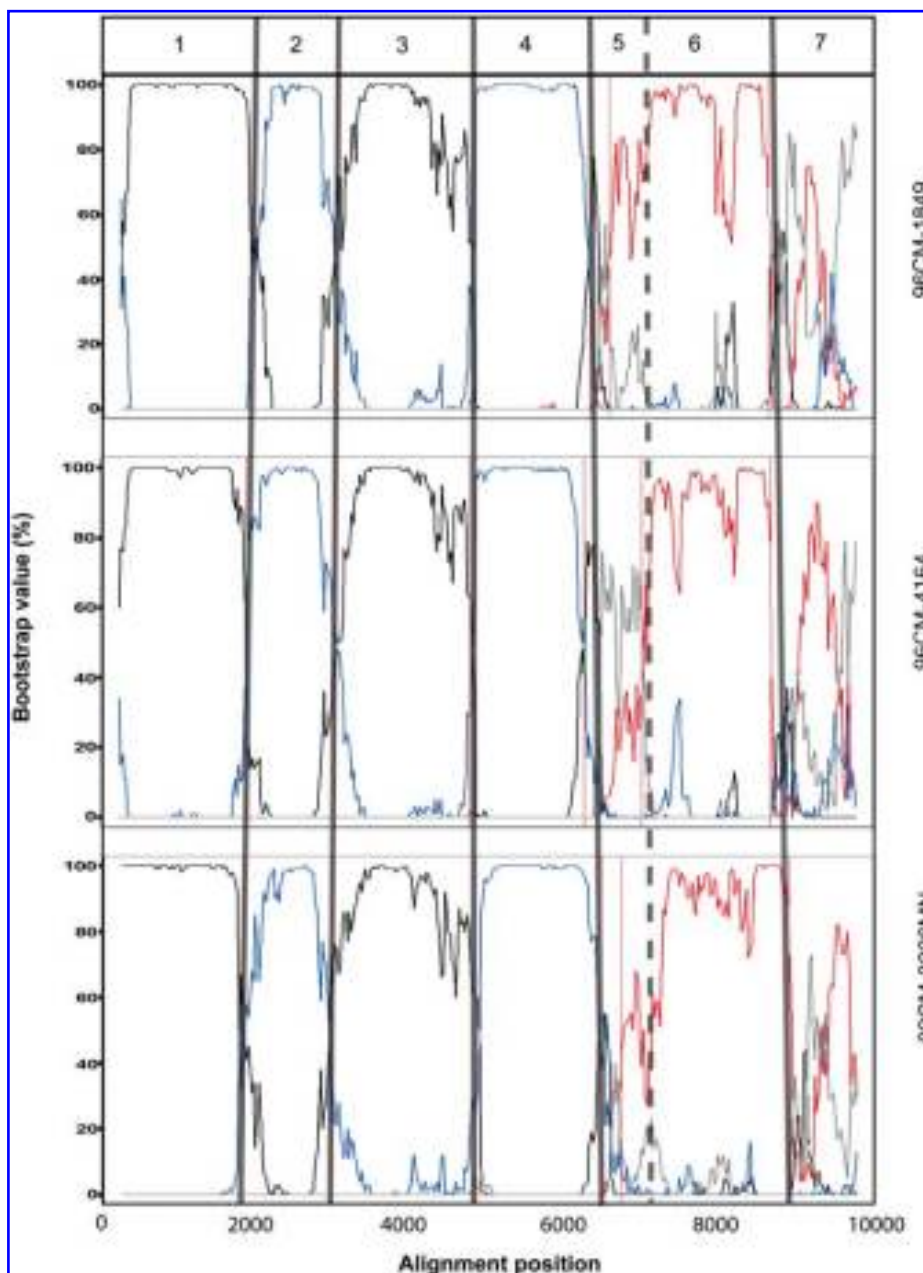


FIG. 1. Bootscanning results of 96CM-1849MN, 96CM-4164MN, and 02CM.3226MN genomes. Nucleotide positions of the alignment are shown on the x-axis and bootstrap values (y-axis) are plotted in the midpoint of each sliding window. The bootstrap values of 96CM-1849MN, 96CM-4164MN, and 02CM.3226MN clustering to subtype G (black), subtype J (blue), subtype A (red), and CRF01-AE (gray) are shown. The vertical lines indicate the breakpoints that divide the genome into the seven fragments (shown in numbers).

branching index, and separate bootstrapped trees for each subtype fragment.

Recombination was first investigated using SimPlot v3.5⁹ (window-size: 400 bp, step-size: 20 bp, 500 replicates) with three different subtype reference sequence sets to avoid effects of bias due to the selection of reference sequences. The first two sets, with one sequence representing each subtype, were selected from the full-length alignment of the HIV sequence database¹⁰ and analyzed independently. The first reference set included (GenBank accession numbers in parenthesis) A1.UG.92.92UG037 (ACC #: U51190), B-US.WR27 (U26546), C.ET.86.ETH2220 (U46016), D.CD.84.84ZR085 (U88822), F1.FR.96.MP411 (AJ249238), F2.CM.95.MP257 (AJ249237), G.FI.93.HH8793_12_1 (AF061641), H.BE.93.VI991 (AF190127), J.SE.94.SE7022 (AF082395), K.CD.97.EQTB11C (AJ249235), and CRF01_H93TH253 (U51189). The second set included AUGSE6594 (AF069672), B-FR.HXB2R (K03455), C.BW.96.96BW0502 (AF110967), D.CD.83.ELI (K03454), F1.BR.93.93BR020_1 (AF005494), F2.CM.95.MP255 (AJ249236), G.SE.93.SE6165 (AF061642), H.BE.93.VI997 (AF190128), J.SE.93.SE7887 (AF082394), K.CM.96.MP535 (AJ249239), and 01_AE.TH.90.CM240 (U54771). The third set included consensus sequences of subtype A–D, F1, F2, G, H, J, K, and CRF01_AE obtained from the HIV sequence

database consensus archive year 2002 (http://www.hiv.lanl.gov/content/hiv-db/CONSENSUS/M_GROUP/Consensus.html).

The similarity plotting and bootscanning analyses revealed that 02CM.3226MN had a mosaic sequence pattern nearly identical to 96CM-1849 and 96CM-4164. On the basis of these preliminary analyses, subtypes A, G, J, and CRF01-AE were included in the subsequent bootscanning analyses in order to more precisely identify the recombination breakpoints of 02CM.3226MN. Figure 1 shows the resulting mosaic structure for all three CRF13 sequences from bootscanning using the consensus sequence as the reference set. Bootscanning analysis results from the two other reference sequence sets corroborated these results (results not shown).

Recombination breakpoints were determined based the bootscanning plots by identification of informative sites and maximization of the χ^2 . As can be seen in Table 1, the breakpoints estimated from each of the three CRF13 sequences individually¹¹ showed some variation. This is not surprising as we would expect the evolution to continue along the CRF13 lineage since its formation, leading to divergence between sequences over time. Thus, a random error will be added and affect our ability to accurately reconstruct the original recombination breakpoints. To address this problem and to better estimate the true breakpoints, we applied a modified version of

TABLE 1. INDIVIDUAL RESULTS FROM SEQUENCE FRAGMENTS OF CRF13 ISOLATES (96CM-1849MN, 96CM-4164MN, AND 02CM.3226MN)

<i>HIV-1 genome</i>	<i>Genome fragment</i>	<i>Fragment (HXB2 position)^a</i>	<i>Potential subtype^b</i>	<i>p value for 3' breakpoint^c</i>	<i>Bootstrap value^d</i>	<i>Branching index</i>
96CM-1849MN	1	623-2312	G	0.0018	100	1.00
	2	2313-3282	J	0.0359	97	0.27
	3	3283-4870	G	0.0096	100	0.86
	4	4871-6258	J	0.0002	92	0.12
	5	6259-6491	? ^e	0.0359	N/A ^f	N/A
	6	6492-8278	A	0.0032	100	1.00
	7	8279-9501	? ^e		N/A	N/A
96CM-4164MN	1	623-2247	G	0.0339	100	1.00
	2	2248-3282	J	0.0544	97	0.27
	3	3283-4870	G	0.0190	100	0.86
	4	4871-6183	J	0.0007	92	0.12
	5	6184-6833	? ^e	0.0226	N/A	N/A
	6	6834-8278	A	0.0013	100	1.00
	7	8279-9430	? ^e		N/A	N/A
02CM.3226MN	1	796-2303	G	0.0339	100	1.00
	2	2304-3282	J	0.1294	97	0.27
	3	3283-4870	G	0.0213	100	0.86
	4	4871-6258	J	0.0013	86	0.12
	5	6259-6483	? ^e	0.0652	N/A	N/A
	6	6484-8278	A	0.0006	100	1.00
	7	8279-9190	? ^e		N/A	N/A

^aThe breakpoints estimated from bootscanning analysis and maximization of chi-square values are shown as corresponding HXB2 positions.

^bThe closest subtype cluster to the analyzed fragment as suggested by maximum likelihood tree analysis.

^cThe probability of the 3' breakpoint of the fragment determined by a chi-square test for heterogeneity of informative sites between adjacent fragments.

^dShown as percentages of 500 neighbor joining trees. For unclassified regions, the bootstrap values are not given.

^eIn these regions the investigated sequences are unclassified, clustering with multiple subtypes. Therefore, BIs are not given.

^fN/A, not applicable.

the standard test that optimizes the breakpoints for all three sequences simultaneously (Fig. 2). Briefly, each phylogenetically informative site supports one of three possible phylogenetic associations among four taxa (the query sequence, two candidate subtypes, and one outgroup) and the χ^2 test is used to locate the maximal difference in the number of informative sites on either side of a putative breakpoint across all sequences simultaneously. Because most sites are uninformative and the informative sites are not evenly distributed, a step-like curve will describe the χ^2 function across sites (Fig. 2). The breakpoint point estimate was chosen as the midpoint of the region with the highest χ^2 value. A region of uncertainty was defined with boundaries given by the location of an informative site that lowered the χ^2 value from the maximum by at least 11 χ^2 units (which in standard statistics correspond to $p < 0.001$).

Each fragment, as suggested by the above breakpoint analysis, was further analyzed individually by maximum likelihood tree analysis for subtype classification (using DNAML in PHYLIP⁷) and by neighbor joining (using PHYLIP as above) for calculating bootstrap values and the branching index as described previously.¹² Year 2001 subtype reference sequences obtained from the HIV sequence database (http://www.hiv.lanl.gov/content/hiv-db/SUBTYPE_REF/align.html) were used in these analyses. A previously defined cutoff value of 0.55, above which subtype designation is supported, was used in this study.¹²

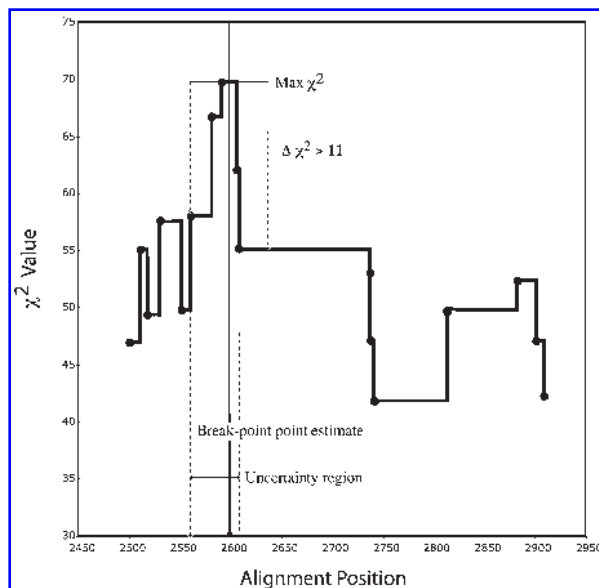


FIG. 2. χ^2 optimization curve and definitions of our breakpoint analysis. Dots on the line mark the positions of informative sites. When a putative breakpoint crosses one such site then the χ^2 value changes, resulting in a discrete step. The breakpoint point estimate is defined as the midpoint of the maximum region in which the χ^2 value does not change (Max χ^2). The region of uncertainty is defined as the range between the two informative sites that lower the Max χ^2 value by at least 11 units. The figure shows the 3'-breakpoint analysis of fragments 2 as an example. Note that the alignment positions are not in HXB2 coordinates at this stage, they are according to our specific alignment.

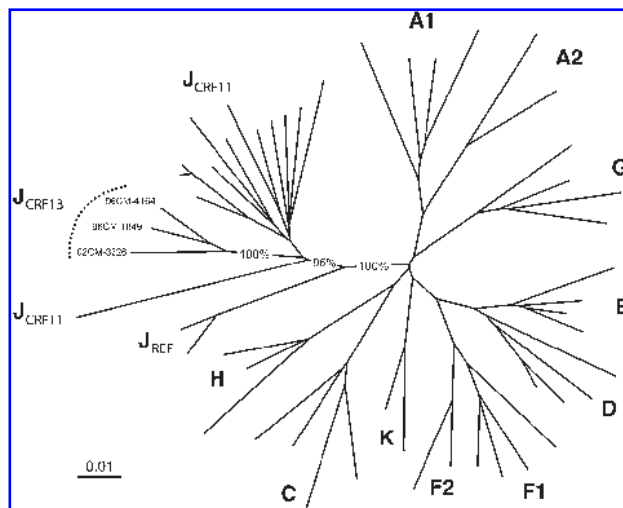


FIG. 3. Maximum likelihood tree of CRF13_cpx (J_{CRF13}), CRF11_cpx (J_{CRF11}), and subtype J reference (J_{REF}) sequences in fragment 2 of CRF13_cpx. The subtype reference sequences¹⁰ and all available sequences from CRF11 and CRF13 were included in the analysis. For simplicity, the individual sequence names were removed and only subtype designations are shown. Bootstrap values are shown for relevant subtype J clades. Based on a BI analysis of subsubtypes A1/A2 and F1/F2 in this genomic region, we hypothesize that subtype J may also be subdivided into J1 (= J_{REF}) and J2 (= $J_{CRF11+CRF13}$). The scale bar indicates 0.01 substitutions/site according to an F84 substitution model.

The genomes of the three CRF13 sequences were divided into seven fragments according to the bootscanning and breakpoint analyses (Fig. 1 and Table 1). Fragment 1 covered most of *gag* and the beginning of *pol* and was classified as subtype G; fragment 2, which included most of *pol* protease, and about half of RT, was classified as subtype J; the other half of RT and most of *pol* integrase (p31) constituted fragment 3 and was identified as subtype G; fragment 4, comprising the last part of *pol* p31 and *vif*, *vpr*, *tat*, *rev*, and most of *vpu*, was classified as subtype J; fragment 5, which included the end of *vpu* and the beginning of *env* gp120, was not clearly associated with any defined subtype, but the majority of *env* that was included in fragment 6 consisted of subtype A1; and finally, fragment 7, which covered the last part of *env*, the second exons of *tat* and *rev*, and most of *nef*, showed a complex pattern with weaker associations to subtypes A, G, and CRF01-AE. In addition, neighbor-joining bootstrap and the branching index (BI) were applied to further test the classification of each fragment. In most fragments, as shown in Table 1, high bootstrap values were consistent with good BI values. For fragments 2 and 4, however, low BI values were observed despite the high bootstrap values. So, fragments 2 and 4, as well as the unclear associations of fragments 5 and 7, were subjected to further analyses.

Fragments 2 and 4 were classified as subtype J based on similarity plotting, bootscanning, and phylogenetic tree analyses. The low BI and the fact that only two J full-length sequences have been sequenced so far, however, raised the question of

TABLE 2. FINAL BREAKPOINTS AND SUBTYPE ASSIGNMENTS OF CRF13_cpx

Fragment	Subtype	3'-Breakpoint ^{a,b}	χ^2 Range ^{a,c}
1	G	2410	2311–2453
2	J2	3146	3115–3163
3	G	4801	4717–5096
4	J1	6169	6032–6283
5	U	6370 ^d	N/A ^e
6	A1	8279	8215–8396
7	CRF01	N/A	N/A

^aPositions are according to HXB2 coordinates.

^bPosition is midpoint estimate of maximum χ^2 region (Fig. 2).

^cRange as defined by $\Delta\chi^2 > 11$ (Fig. 2).

^dBreakpoint estimated by bootstrap support <70%; see text for details.

^eN/A, not applicable.

whether these two J reference sequences were good representatives of subtype J. Thus, 96CM-1849MN, 96CM-4164MN, and 02CM.3226MN were compared with all possible J-containing CRFs (queried from Los Alamos HIV sequence database) in regions corresponding to fragments 2 and 4, respectively, again using similarity plotting, bootscanning, and phylogenetic tree reconstruction.

Among other described CRFs besides CRF13_cpx, only CRF11-cpx has a J part in the region of fragment 2 of CRF13_cpx. The maximum likelihood tree result demonstrated that fragments 2 from 02CM.3226MN, 96CM-1849MN, and 96CM-4164MN clustered with CRF11-cpx rather than the subtype J reference sequences (Fig. 3). This showed that the J fragments of CRF13 and CRF11-cpx are more closely related to each other than to the subtype J reference sequences in the region of fragment 2 of CRF13, which is also consistent with the previous result.⁶ Thus, this suggests that fragment 2 of CRF13 and CRF11 may have originated from a common ancestor. An analysis of BIs in fragment 2 showed that J(ref) and J(CRF11 + CRF13) related to each other in a similar way as does A1 to A2 and F1 to F2 ($BI_{A1/A2} = 0.35$; $BI_{A2/A1} = 0.55$; $BI_{F1/F2} = 0.46$; $BI_{F2/F1} = 0.67$; $BI_{J(ref)/J(CRF)} = 0.35$; $BI_{J(CRF)/J(ref)} = 0.63$). Thus, although it is somewhat unclear which of the subtypes should be regarded as the “main” cluster, subtype J

sequences in CRF11 and CRF13 seem to have derived genomic material from J clade representatives as diverse as subsubtypes are. This may indicate that a subsubtype J2 may exist or have existed when CRF11 and CRF13 were created.

A similar analysis was performed for fragment 4 of CRF13_cpx and other J-containing CRFs (CRF06 and CRF11) in the corresponding region. The J fragment in this region covers HXB2 positions 4096–6048 in CRF06 and 5058–5454 and 5848–6258 in CRF11. Hence, the J segments covered by CRF06, CRF11, and CRF13 within fragment 4 were 5058–5454 and 5848–6048. In contrast to fragment 2, in fragment 4 no closer association was detected to other J-containing CRFs than to the standard reference J sequences (data not shown).

Fragments 5 and 7 showed weak similarities with any of the reference sequences (Fig. 1). The phylogenetic analyses also did not reveal clear classification of these two fragments with any other subtypes⁶ (data not shown). Our new sequence, 02CM.3226MN, was intensely investigated in fragment 5 because the span of this fragment was somewhat ambiguous among the three sequences (Fig. 1 and Table 1). Thus, fragment 5 was broken into two smaller parts based on an additional breakpoint according to the results from all three CRF13 sequences (Fig. 1). The first part (HXB2 positions 6183–6376) showed that all three CRF13 were more similar to CRF01 instead of to subtype G as shown in the bootscanning plot (Fig. 1). Awkwardly, however, CRF01 shared a most recent common ancestor with subtype G split by the CRF13 sequences. In the phylogenetic analysis of the second part (6377–6811), CRF13 isolates did not show close relation with CRF01, which was again inconsistent with the bootscanning results. Also unexpected in this tree was that subtype J clustered inside subtype G. All these results were supported by good bootstrap results. Considering the unsatisfactory tree results, most likely explained by the short lengths of these two parts within fragment 5, we left fragment 5 unclassified. To determine the breakpoints, i.e., the start and end of fragment 5, we could not use the above described χ^2 method, however. Instead, and to be conservative, the 3'-boundary of this region was determined by the right-most position among the three CRF13 sequences where the bootstrap fell below 70% (HXB2 position 6370). To justify this bootstrap method, the ranges of where the bootstrap fell below 70% in each of the three sequences were compared to the results of the overall χ^2 method at all other breakpoints, and reassuringly it was found to agree very well (data not

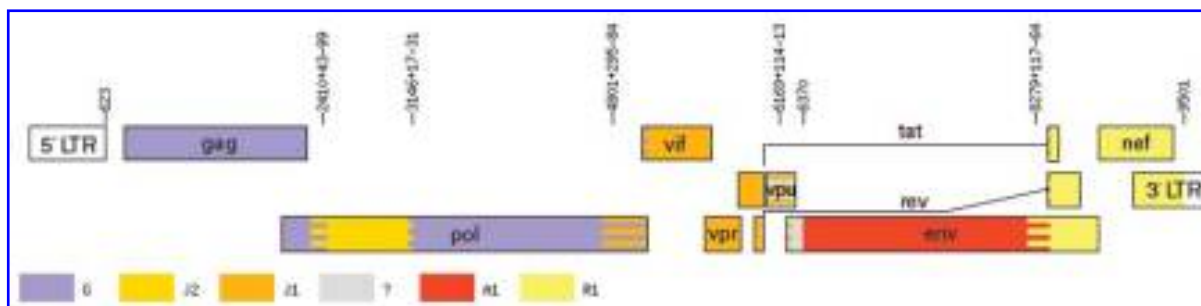


FIG. 4. Mosaic subtype organization of CRF13_cpx. Breakpoints are according to the HXB2 numbering system, and uncertainty regions are shown as interlaced fields. The colored fields correspond to subtype designations; R1 in the figure stands for CRF01. This map was generated using Recombinant HIV-1 Mapper, a new tool at the Los Alamos HIV database.

shown). Thus, this seemed to be a reasonable alternative to define the range of unclassified sequence regions. Finally, fragment 7 was reanalyzed and found most closely associated with CRF01 (data not shown). The low bootscanning curves were explained by the fact that fragment 7 contained subtype A parts that caused competition between subtype A and CRF01 references, as previously reported.⁶

The resulting breakpoints and subtype classifications after our reanalysis of CRF13 are shown in Table 2 and Fig. 4. The breakpoints are estimates of the parental CRF13 with regions of uncertainty. It is expected that when more full genomes become available, the breakpoints will be better estimated and the uncertainty region will become closer to a true confidence interval.

It has been reported that both 96CM-4164MN and 96CM-1849MN have an insertion of 10 amino acids (SRPEPTAPPA) in *gag* p6 (corresponding to amino acids 460/461 in HXB2), and this insertion is unique for these isolates.⁶ Here we found that 02CM.3226MN had almost the same insertion of SRPEPTAPPV in this region. However, a number of subtype B and C sequences have similar inserts in this region, which seems to be due to a repetitive element. Thus, although all three CRF13 sequences have this insert, it is not as unique as was originally suggested.

In conclusion, the new isolate 02CM.3226MN was classified as the third member of the CRF13 family. The subtype fragment ranges were somewhat revised to the previously reported CRF13_cpx's sequences (Fig. 4). A modified χ^2 breakpoint analysis was applied to optimize breakpoints across all available sequences, improving the accuracy as well as adding a measure of certainty to the analysis of breakpoint locations. In fragment 2 high bootstrap values coexisted with low branching index values. Our explanation for this discrepancy is that the two standard reference J sequences may not be good representatives of this J-containing CRF. Instead, CRF13 and CRF11 were closer to each other in this fragment. Because no such relation was observed in fragment 4, however, the picture is more complicated. It is possible that CRF13 got material from both what is represented by the subtype J reference sequences (J1) and as of now undiscovered representatives of subsubtype J2. Indeed, the lack of more J reference sequences confounds the identification and analysis of mosaic genomes, in particular in areas where multiple sequence subtypes and CRFs co-circulate (like Cameroon from which all CRF13 were sampled).

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