The complete genome of a baculovirus isolated from an insect of medical interest: *Lonomia obliqua* (Lepidoptera: Saturniidae)

C. W. Aragão-Silva\(^1\), M. S. Andrade\(^1\), D. M. P. Ardisson-Araújo\(^1\), J. E. A. Fernandes\(^1\), F. S. Morgado\(^1\), S. N. Bário\(^1\), R. H. P. Moraes\(^3\), J. L. C. Wolff\(^2\), F. L. Melo\(^1\) & B. M. Ribeiro\(^1\)

*Lonomia obliqua* (Lepidoptera: Saturniidae) is a species of medical importance due to the severity of reactions caused by accidental contact with the caterpillar bristles. Several natural pathogens have been identified in *L. obliqua*, and among them the baculovirus *Lonomia obliqua* multiple nucleopolyhedrovirus (LoobMNPV). The complete genome of LoobMNPV was sequenced and shown to have 120,022 bp long with 134 putative open reading frames (ORFs). Phylogenetic analysis of the LoobMNPV genome showed that it belongs to *Alphabaculovirus* group I (lepidopteran-infective NPV). A total of 12 unique ORFs were identified with no homologs in other sequenced baculovirus genomes. One of these, the predicted protein encoded by *loob035*, showed significant identity to an eukaryotic transcription terminator factor (TTF2) from the Lepidoptera *Danaus plexippus*, suggesting an independent acquisition through horizontal gene transfer. Homologs of *cathepsin* and *chitinase* genes, which are involved in host integument liquefaction and viral spread, were not found in this genome. As *L. obliqua* presents a gregarious behavior during the larvae stage the impact of this deletion might be neglectable.

Although the vast majority of caterpillars species do not represent a threat to human health, members of 12 lepidopteran families may cause serious human injuries\(^1\). Among these, the larvae *Lonomia obliqua* (Walker, 1855) (Lepidoptera: Saturniidae) is included, causing several accidents in the Southern region of Brazil\(^2\). This insect has been detected feeding on plants from the families *Anacardiaceae* and *Meliaceae* and in city orchards\(^2\). When in contact with the human skin, a toxin is released by the larvae bristles, resulting in reactions varying from local irritation to severe life threatening conditions such as coagulopathy, acute renal failure and hemorrhagic disorders\(^3\). The gregarious nature of the larvae contributes to a higher venom exposure, which aggravates the severity of the symptoms. There are indications that the occurrence of accidents with *L. obliqua* is increasing\(^2\), possibly due to several factors such as deforestation, the introduction of exotic plants and reduction of natural enemies\(^4\).

The need to control this insect population has led to the identification of several pathogens and predators, including a nematode (*Hexamermis sp.*)\(^5\) and a baculovirus: *Lonomia obliqua* multiple nucleopolyhedrovirus (LoobMNPV), which was isolated from *L. obliqua* larvae\(^6\). The infected larvae exhibited all the usual symptoms of a baculovirus infection, although lacking liquefaction and melanization post mortem phenotypes\(^6\). A previous study determined the sequence of a conserved baculovirus gene (*polyhedrin*) gene that showed close similarity with members of group I alphabaculoviruses\(^6\).

The first baculovirus to be completely sequenced was the *Autographa californica* multiple nucleopolyhedrovirus (AcMNPV) in 1994\(^7\). Since then, the number of complete genomes has been growing rapidly, providing a wealth of data that contributes to the understanding of both biology and evolution of baculoviruses. However, there are only three reports of complete genomes from baculoviruses isolated from species of the family Saturniidae: *Hemileuca sp. nucleopolyhedrovirus*\(^8\), *Philosamia cynthia nucleopolyhedrovirus*\(^9\), and two isolates of *Antheraea*...
pernyi nucleopolyhedrovirus\textsuperscript{10}. Therefore, the complete genome of LoobMNPV provides additional data that may help the understanding of baculovirus genome evolution and adaptations to their hosts.

**Results and Discussion**

**Genome Features.** The assembled genome of LoobMNPV (GenBank accession number: KP763670) is 120,023-bp long with a mean coverage of 20.5 times. We have found 134 Open Reading Frames (ORFs) coding for putative proteins with at least 50 amino acid residues (Fig. 1a and Table S1). Out of these, 120 ORFs were found in other baculoviruses and among those, three ORFs (loob078, loob100 (he65) and loob113) showed higher identity with orthologs from betabaculoviruses (Table S1), confirming that horizontal transference between alphabaculovirus and betabaculovirus is indeed a common event, as previously documented\textsuperscript{11}. Moreover, some unique ORFs were located within the hr3 (loob038) and hr4 (loob060 and loob061). All the 37 baculovirus core genes were present, however some genes present in almost all Alpha- and Betabaculovirus\textsuperscript{12} genomes available were not present: Ac106/107, Ac108 and gp37.

**LoobMNPV homologous regions (hrs).** Seven homologous regions (hrs) were found in the LoobMNPV genome, in agreement to other baculoviruses\textsuperscript{13}. These DNA palindromic repetitive elements are interspersed throughout most baculoviral genomes and are related to DNA replication\textsuperscript{14}, gene transcription\textsuperscript{15}, and possibly homologous recombination\textsuperscript{16}. The hr1 has 684 bp, hr2 has 541 bp, hr3 has 1,037 bp, hr4 has 1,426 bp, hr5 has 679 bp, hr6 has 361 bp and hr7 has 836 bp, and their size and position were confirmed by PCR (data not shown). As shown in Fig. 2, all hrs have various copies of a common imperfect palindromic repeat of 38 bp (hr1a, hr2a, hr3a, hr3b, hr4a, hr5a, hr5b, hr6a, hr6b and hr7a).

**LoobMNPV Phylogeny.** We have performed a phylogenetic analysis (Fig. 3) based on the concatenated amino acid sequence alignment of 37 baculovirus core genes of 72 baculovirus species available in GenBank (Table S2). LoobMNPV clustered with group I alphabaculovirus. Its closest relative was found to be DekiNPV and both are basally related to AcMNPV-like viruses. This result disagrees with previous analysis based on the
polh gene, in which LoobMNPV clustered together with both species *Amsacta albistriga nucleopolyhedrovirus* (AaNPV) and *Thysanoplusia orichalcea nucleopolyhedrovirus* (ThorNPV). However, the phylogenetic signal of highly conserved genes, such as *polh*, is usually inaccurate, while phylogenetic inferences based on a large set of genes is more accurate and robust.

**LoobMNPV Comparative Genomics.** Based on the phylogenetic results we have selected some of the closest relatives of LoobMNPV, including AcMNPV, *Antheraea pernyi nucleopolyhedrovirus* (AnpeNPV), *Maruca vitrata nucleopolyhedrovirus* (MaviNPV), *Dendrolimus kikuchii nucleopolyhedrovirus* (DekiNPV) and ThorNPV for comparative genomics. Figure 1b and Table S1 reveal all the LoobMNPV ORFs compared to orthologs from these genomes by the level of similarity (in terms of percentage of identity and *E*-values < 10⁻³). Overall, some
ORFs are more conserved (high similarity), such as the genes that correspond to polh (loob001), p74 (loob010), p49 (loob014), pif-1 (loob041), vif-1 (loob067), lef-9 (loob080), lef-8 (loob093) and pif-2 (loob123); while others are more variable, presenting a lower level of similarity, but still present in almost all baculovirus genomes, such as ORF1629 (loob002), ie-2 (loob005), vp80 (loob043), desmoplakin (loob075), f protein (loob122), arif-1 (loob124) and bv/odv-e26 (loob128).

Moreover, we have investigated the genome synteny among LoobMNPV and those selected alphabaculovirus genomes (Fig. 4). A circular ideogram layout shown in Fig. 4 displays lines connecting related genes, where it is possible to observe the relative position compared to LoobMNPV genome. Interestingly, we have observed that LoobMNPV and DekiNPV show high collinearity, and both present genome inversions and rearrangement in contrast to the genomes of AcMNPV, AnpeNPV, MaviNPV, and ThorNPV. The inverted regions were adjacent or flanked by the hr1 and hr2 (Fig. S1). These findings support the phylogenetic results presented in Fig. 3 and suggests that the inversions were originated in a common ancestor of both LoobMNPV and DekiNPV. These inversions are an autapomorphy when compared to the AcMNPV-like viruses. Previous studies have shown that rearrangements in the baculovirus genomes reflect evolutionary history, with more closely related viruses presenting higher genome collinearity.

Furthermore, when analyzing the region where all genomes overlap with LoobMNPV (Fig. 4b), we have observed that unique ORFs in LoobMNPV (gaps with no correspondence to the other genomes) are interestingly
found near hrs. According to previous reports, gene rearrangements and acquisitions are of common occurrence on proximities of hrs, confirming the possibility of gene transfers to viruses by homologous recombination, which could be also facilitated by factors such as the prevalence of various pathogens infecting the same host, as well as concomitant infections in field populations.

**LoobMNPV unique ORFs.** LoobMNPV genome showed 12 genes that do not have any match among baculoviruses. These ORFs are loob004, loob006, loob012, loob035, loob038, loob055, loob059, loob060, loob061, loob071, loob084, and loob097. There are three possible mechanisms for gene acquisition: extensive sequence divergence, which could push homolog genes below the similarity threshold; gene recombination, which produces novel protein products; and horizontal gene transfer (HGT). This third possibility is expected to be detectable by gene similarity from phylogenetically distinct species. For each of these LoobMNPV unique ORFs, we have searched for baculovirus promoter motifs within 200 bp upstream of the start codon. The late promoter motif TAAG, that appears to be necessary for late transcription by the viral RNA polymerase was found in loob004, loob012, loob030, loob038, loob055, and loob071. However, further experiments are necessary to confirm whether these ORFs encode bona fide proteins. Moreover, these novel ORFs were searched for known domains and eight of these ORFs (loob004, loob006, loob012, loob038, loob055, loob061, loob071, and loob097) did not match any predicted domain. The remaining will be discussed below.

**Insect immune system-associated domain.** The loob060 has an immunoglobulin-like domain, which has been found in some insect proteins, such as the hemolin, an hemolymph component that plays a role in bacterial surface binding, forming a protein complex that initiates the immune response. Hemolin has also been found in the transcripts of L. obliqua bristles. Several immunomodulators encoded by viruses have been described and may be involved in regulating the immune system and protecting virus-infected cells from the attack of other cells from the immune system. For viruses, the expression of these proteins may indicate beneficial susceptibility in multiple pathogen infections, by protecting the host against opportunistic pathogens, reducing competition and benefiting viral propagation. For instance, other saturniid-related alphabaculovirus species HespNPV expresses a functional insect-related serine protease inhibitor (serpin) in its genome that is likely related to host immunity modulation and virulence.

**Transcription factor-related domain (loob035).** One unique ORF demonstrated high correspondence to the eukaryotic transcription terminator factor type 2 (TTF2) from the butterfly Danaus plexippus (GenBank: EHJ68439), with 44% pairwise identity and E-value equals to $3e^{-11}$. However, when filtering this result, in order to focus only on the family Baculoviridae, the referred gene presented higher similarity to the Global Transactivator (GTA) gene from the AnpeNPV (YP_611073), with 66% of identity and an E-value of $1e^{-9}$. Transcription Factors (TFs) in general are fundamental in a broad array of any cellular processes due to its ability of causing changes in downstream gene expression patterns. GTA genes are observed in members from the group I Alphabaculovirus. According to a previous study, baculovirus GTAs play an important role in transcriptional activation of viral genes and were probably originated by HGT from the host to the common ancestor of the clade that includes AcMNPV, Bombyx mori nucleopolyhedrovirus (BmNPV), Orgyia pseudotsugata multicapsid nucleopolyhedrovirus (OpMNPV), and Epiphyas postvittana nucleopolyhedrovirus (EppoNPV). Katsuma, et al. found that a GTA homolog from BmNPV acts as a viral virulence factor in insect larvae, and may be required for activation of host and/or viral genes, increasing the speed of host killing. Based on domain analysis, we have found that the loob035, TTF2, and GTA genes are members of the SNF2 family. This family of genes encodes proteins with sequence motifs similar to those found in many DNA and RNA helicase protein families, and also proteins from a variety of species with roles in cellular processes such as transcriptional regulation, DNA recombination, chromatin unwinding and various other types of DNA repair. In this regard, the possible acquisition of loob035 might be involved in the inhibition of the host transcriptional machinery in order to benefit viral expression.

To analyze whether loob035 has been independently acquired from the host insect through HGT, or is a divergent baculovirus GTA gene, a phylogenetic analysis has been performed, based on an amino acid alignment containing both TTF2 and GTA sequences. As shown in Fig. 5, loob035 presented a long branch size, which
indicates great divergence from the other sequences, possibly due to positive selection34. Actually, TFs are over-represented among genes predicted to be positively selected in previous genome-wide selection studies35. To confirm whether loob035 is in fact a new acquisition from insect host or a divergent baculovirus GTA gene, we compared the likelihood of a tree constraining loob035 to the GTA alphabaculovirus group (lnL = −14940.61) with the likelihood of a tree constraining loob035 into TTF2 group (lnL = −1455.06). We argue that the likelihood differences in combination with high non-parametric bootstrap values and high posterior probabilities constitute considerable evidence that loob035 clusters with the group of TTF2 genes, corroborating to the possibility of a novel HGT.

We further confirmed this independent acquisition hypothesis by analyzing the genomic context of baculovirus GTA genes. As shown in Fig. 6a, GTA genes are encountered in all group I Alphabaculovirus and is shown here aligned to the phylogeny previously showed on Fig. 3. In AcMNPV, AgMNPV, AnpeNPV, BmNPV, BomaNPV, CfMNPV, ChocNPV, ChmuNPV, ChroNPV, DekiNPV, EppoNPV, HycuMNPV, LoobMNPV, MaviMNPV, OpMNPV, PhcyNPV, PlxyMNPV, RoMNPV e ThorNPV, the GTA gene is always in between p-47 (followed by lef-12) and odv-e56. LoobMNPV, DekiNPV and MaviMNPV lack the GTA gene. Dotted lines represent absence of ORFs. (b) The position of loob035 in the genome of LoobMNPV is located between homologs of both ac110-like (loob034) and ac111-like (loob036). The position of two loob035 homologs (Table S1) from DekiNPV_Orf138 and ThorNPV_Orf117 are also represented in different genome contexts.

Figure 6. GTA genomic context in several alphabaculoviruses. (a) The GTA gene is present in almost all group I Alphabaculovirus and is shown here aligned to the phylogeny previously showed on Fig. 3. In AcMNPV, AgMNPV, AnpeNPV, BmNPV, BomaNPV, CfMNPV, ChocNPV, ChmuNPV, ChroNPV, DekiNPV, EppoNPV, HycuMNPV, LoobMNPV, MaviMNPV, OpMNPV, PhcyNPV, PlxyMNPV, RoMNPV e ThorNPV, the GTA gene is always in between p-47 (followed by lef-12) and odv-e56. LoobMNPV, DekiNPV and MaviMNPV lack the GTA gene. Dotted lines represent absence of ORFs. (b) The position of loob035 in the genome of LoobMNPV is located between homologs of both ac110-like (loob034) and ac111-like (loob036). The position of two loob035 homologs (Table S1) from DekiNPV_Orf138 and ThorNPV_Orf117 are also represented in different genome contexts.
(ChmuNPV), Choristoneura nucleopolyhedrovirus roacea (ChroNPV), EppoNPV, Hyphantria cunea nucleopolyhedrovirus (HycuMNPV), Orgyia pseudotsugata multicapsid nucleopolyhedrovirus (OpMNPV), Philosia cynthia nucleopolyhedrovirus (PhcyNPV), Platella xylostella multiple nucleopolyhedrovirus (Px2yMNPV), Rachiphusia ou multicapsid nucleopolyhedrovirus (RoMNPV) and ThorNPV, except in MaviMNPV, LoobMNPV and DekiMNPV, within a conserved position between hr1 and odv-66. However, in LoobMNPV, the gene located in this position is loob102, that corresponds to an AcMNPV-like gene (ac044). On the other hand, loob035 is inserted in a completely different genome context, located between both the ac110and the ac111-like genes (Fig. 6b), confirming that loob035 has probably a different origin not related to the GTA gene. Besides, loob035 homologs found in DekiMNPV (Orf 138) and in ThorNPV (Orf 117), according to Table S1, are also inserted in a different context (Fig. 6b).

Notably, loob035 diverges greatly from all the other compared sequences (Fig. S2), showing that these sequences present similarity only because they all contain the SNF2 conserved domain. Hughes & Friedman found that SNF2 baculovirus gene family has homologs in cellular organisms, and clustered closer to homologs in insects (Drosophila), according to the reconstruction of the evolutionary relationship among genes that were potentially acquired through HGT in comparison to baculovirus phylogeny.

The absence of cathepsin and chitinase genes in LoobMNPV. Interestingly, LoobMNPV does not encode two common baculovirus genes that are responsible for the post mortem host melanization and liquefaction benefitting virus dissemination: the enzymes cathepsin (v-cath) and chitinase (chiA) genes. Besides the involvement of these genes in the horizontal spread of the virus in the field, it has been reported that the chiA gene and the pro-form of v-cath interact directly and are dependent on each other for the promotion of host liquefaction, and therefore, they are usually acquired or lost together. Among alphabaculoviruses from group I, only LoobMNPV, AgMNPV and PhcyNPV lack v-cath and chiA genes. The recombinant introduction of v-cath and chiA genes from Choristoneura fumiferana DEF multiple nucleopolyhedrovirus (CDEFNFPV) into AgMNPV genome improves production of occlusion bodies and insecticidal activity during A. gemmatalis larvae infection.

Several hosts from the family Saturniidae, as well as from Noctuidae, present gregarious behavior, which may facilitate virus dispersion to new susceptible individuals and reduce selective pressure for the maintenance of v-cath and chiA genes, as observed for LoobMNPV, AgMNPV, and PhcyNPV. However, HespNPV and AnpeNPV also infect gregarious hosts from Saturniidae family, but have v-cath and chiA genes in their genomes. Therefore, it remains to be determined whether the host behavior it is indeed a selective factor for cath and chiA genes maintenance.

Conclusions. In this work, we described the first complete genome sequence of a baculovirus isolated from a species of medical interest. LoobMNPV is located on a basal position of group I alphabaculovirus and presents inversions in large proportions when compared to the other related genomes. During evolution, fluxes in the genomes content, such as genes acquisitions and losses, pressured by positive selection, could possibly implicate inversions in large proportions when compared to the other related genomes. During evolution, the novel genomes will help the studies on baculovirus evolution, proportioning deeper knowledge and understanding of baculovirus as a whole group.

Materials and Methods

Virus origin. The LoobMNPV used in this work was collected in the year 2000, from orchards in the state of Santa Catarina, Brazil.

Virus purification, DNA extraction and sequencing. Occlusion bodies (OBs) from dead L. obliqua larvae were purified and dissolved in an alkaline solution for DNA purification, all according to previously published protocol to O’reilly et al. The quantity and quality of the DNA was determined by electrophoresis on 0.8% agarose gel (data not shown). The DNA was submitted to genome sequencing throughout the pyrosequencing technique performed by the 454 Genome Sequencer (GS) FLX™ Standard (Roche) at Macrogen Inc (Seoul, Republic of Korea).

Genome assembly and annotation. Genome de novo assembly and annotation was performed using Geneious version 7.1.6 (available at http://www.geneious.com/) considering the following established parameters to select the Open Reading Frames (ORFs): start codons corresponding to the methionine residue (ATG), minimal overlapping of adjacent ORFs, and ORFs as large as 150 bp. No gaps were found between connected contigs, only a 700 bp region of low coverage, that was confirmed by PCR. In order to validate assembly, an in silico digestion was carried out using BamHI, EcoRI and PstI restriction enzymes and comparing to a previously published restriction profile, that used the same virus isolate as the one used in this work (Table S3). ORFs were annotated using BLASTx and PSI-BLASTp searches against the NCBI non-redundant protein database. When compared to all baculoviruses genomes available at Genbank, unique ORFs were considered when no significant database hits (E-values > 1 x 10^{-3}) were found, and for those, a more sensitive search was performed using HMmer-search against the PFAM-database. The presence of protein specific domains in HMMer-search-unique ORFs was investigated using InterProScan database. The regions within 200 bp upstream of the putative unique ORFs were screened for the presence of TATA-box and CAGT motifs, as well as GATA motifs.

Homologous regions (hrs). The homologous regions (hrs) were annotated using DOTPLOT analysis and Tandem Repeat Finder (http://tandem.bu.edu/trf/trf.html). An alignment of the repeat unit of each hr was performed using the MAFFT method. To confirm the size and position of the hrs among the genome, PCRs were performed, using the isolated LoobMNPV DNA and the following primers: hr1 (F: AGA GTT GGA AAT TTC
Phylogenetic analysis and genome comparisons. A MAFFT alignment was performed using amino acid sequences from the predicted 37 core genes from 72 baculovirus genomes (one isolate from each baculovirus species) available in the GenBank up to the date. The phylogeny was inferred by three different phylogenetic algorithms including FastTree51, which uses SH-like method for branch support, along with RAxML52 and PhyML53 that use the bootstrap method for branch support. The phylogenies were inferred by the maximum likelihood (ML) method, along with GTR model of DNA evolution, estimated with JmodelProttest 2.4 software program54. Moreover, a genomic comparison was performed using blastp identity results of a protein dataset with four alphabaculovirus genomes AcMNPV, AnpeNPV, MaviNPV, and ThorNPV. This dataset was compared using CGView Comparison Tool55 and the results were plotted using CIRCOS56. Likewise, to investigate the evolutionary relationship between loob035 and the GTA and TTF2 genes, a MAFFT alignment was performed using 14 GTA genes from alphabaculoviruses and 62 TTF2 genes from insects and other eukaryotes. This phylogenetic tree was done by ML method implemented in PhyML53, with JTT substitution model of amino acid evolution, and 100 repetitions of a non-parametric bootstrap. A multiple alignment was performed on the T-coffee platform57 with the predicted loob035 along with the GTA and TTF2 proteins, and was submitted to the ESPript 3 platform58. The two most similar crystal structures to loob035 were used to predict the secondary structures of the alignment. They were extracted from the Protein Data Bank (PDB ID 3mwy59 and PDB ID 1z6360), and were aligned along with the GTA and TTF2 genes using Tfastp60. To show statistical evidence concerning the best hypothesis for loob035 position in the GTA/TTF2 tree, the Bayes factor estimator61 from MrBayes program62 was used.

References
1. Diaz, J. H. The evolving global epidemiology, syndromic classification, management, and prevention of caterpillar envenoming. Am. J. Trop. Med. Hyg. 72, 347–357 (2005).
2. Carrijo-Carvalho, L. C. & Chudzinski-Tavassi, A. M. The venom of the Lonomia caterpillar: an overview. Toxicicon 49, 741–757 (2007).
3. Gamborgi, G. P., Metcalf, E. B. & Barros, E. J. G. Acute renal failure provoked by toxin from caterpillars of the species Lonomia obliqua. Toxicicon 47, 68–74 (2006).
4. Abella, H. B. et al. Manual de diagnóstico e tratamento de acidentes porLonomia.20 (Centro de Informação Toxicológica-SS/RS-FEPES, 1999).
5. Moraes, R. H. P. Identificação dos Inimigos Naturais de Lonomia obliqua Walker, 1855 (Lepidóptera: Saturniidae) e possíveis fatores determinantes do aumento de sua população. Masters Thesis, Escola Superior de Agricultura Luiz de Queiroz (2002).
6. Wolff, J. L., Moraes, R. H. P., Kitaizima, E., Leal, E. D. S. & Zanotto, P. M. A. Identification and characterization of a baculovirus from Lononmia obliqua (Lepidoptera: Saturniidae). J. Invertebr. Pathol. 79, 137–145 (2002).
7. Ayres, M. D., Howard, S. C., Kuzio, J., Lopez-Ferber, M. & Posser, R. D. The complete DNA sequence of Autographa californica ortholog. Virus Genes 47, 357–64 (2013).
8. Qian, H. et al. Analysis of the genomic sequence of Philosamia cynthia nucleopolyhedrin virus and comparison with Antheraea pernyi nucleopolyhedrovirus. BMC Genomics 14, 115 (2013).
9. Nie, Z. M. et al. Complete sequence and organization of Antheraea pernyi nucleopolyhedrovirus, a dci-rich baculovirus. BMC Genomics 8, 248 (2007).
10. Ardisson-Araújo, D. M. P. et al. Genome sequence of Erinnys ello granulovirus (ErelGV), a natural cassava hornworm pesticide and the first sequenced sphingid-infecting betacullovirus. BMC Genomics 15, 856 (2014).
11. Garavaglia, M. I., Miele, S. A., Iserte, J. A., Belaich, M. N. & Ghiorgielli, P. D. Ac5, ac78, ac101 and ac103 are newly discovered core genes in the family Baculoviridae. J. Virol. 86, 12069–12079 (2012).
12. Oliveira, J. V. et al. Genome of the most widely used viral biopesticide: Anticarsia gemmatalis multiple nucleopolyhedrovirus. J. Gen. Virol. 87, 3233–3250 (2006).
13. Pearson, M. N. & Rohrmann, G. F. Lymantria dispar nuclear polyhedrosis virus homologous regions: characterization of their ability to function as replication origins. J. Virol. 71, 213–221 (1997).
14. Fang, Y. et al. Sequence analysis of the Spodoptera litura multicanal nucleopolyhedrovirus genome. Virology 287, 391–404 (2001).
15. Hayakawa, T. et al. Sequence analysis of the Xestia c-nigrum granulovirus. Virology 262, 277–297 (1999).
16. Jelhe, J. A. et al. On the classification and nomenclature of baculoviruses: a proposal for revision. Arch. Virol. 151, 1257–1266 (2006).
17. Herniño, E. A., Olszewski, J. A., Cory, I. S. & O’Reilly, D. R. The genome sequence and evolution of baculoviruses. Annu. Rev. Entomol. 48, 211–234 (2003).
18. Hu, Z. et al. Distinct gene arrangement in the Buzura suppressaria single-nucleocapsid nucleopolyhedrovirus genome physical map was constructed for the restriction. J. Gen. Virol. 79, 2841–2851 (1998).
19. Thumib, D. K., Bèlèvè, C., Cuossè, M., Lapointe, R. & Lucottèi, C. J. Comparative genome sequence analysis of Choristoneura accidens Freeman and C. rosaceana Harris (Lepidoptera: Tortricidae) alphabaculoviruses. PLoS One 8, e68968 (2013).
20. De Jong, J. G. et al. Analysis of the Choristoneura fumiferana nucleopolyhedrovirus genome. J. Gen. Virol. 86, 929–943 (2005).
21. Eveleigh, E. S. et al. Fluctuations in density of an outbreak species drive diversity cascades in food webs. Proc. Natl. Acad. Sci. USA 104, 16976–16981 (2007).
22. Kempe, E. M., Woodward, D. T. & Cory, I. S. Detection of single and mixed cocovirus infections in eastern spruce budworm, Choristoneura fumiferana populations. J. Invertebr. Pathol. 107, 202–205 (2011).
23. McListaght, A., Baldi, P. F. & Gau, B. S. Extensive gene gain associated with adaptive evolution of poxviruses. Proc. Natl. Acad. Sci. USA 100, 15655–15660 (2003).
24. Garry, T. B., Chang, M. J. & Blussard, G. W. Late Promoter Selection in the Baculovirus gp64 Envelope Fusion Protein Gene. Virology 231, 167–181 (1997).
25. Sun, S. C., Lindstrom, I., Boman, H. G., Faye, I. & Schmidt, O. Hemolin: An Insect-Immune Protein Belonging to the Immunoglobulin Superfamily. Science 250, 1729–1732 (1990).
The authors declare no competing financial interests. The additional information accompanies this paper at http://www.nature.com/srep.

Author Contributions

de Pessoal de Nível Superior’ (CAPES).

Acknowledgements

We thank the Ministry of Science, Technology and Innovation, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq): Grant number 407908/2013-7; Fundação de Apoio à Pesquisa do Distrito Federal -FAPDF: Grant number 193.000.583/2009 for financial support and ‘Coordenação de Aperfeiçoamento de Pessoal de Nível Superior’ (CAPES).

Author Contributions

C.W.A.S., D.M.P.A., F.L.M., J.L.C.W., M.S.A. and B.M.R. wrote the main manuscript text. D.M.P.A., F.L.M., S.N.B., J.E.A.F. and B.M.R. designed and conceived the experiments. C.W.A.S., D.M.P.A., F.L.M., J.E.A.F., F.S.M., M.S.A. and R.H.P.M. performed experiments. All authors reviewed the manuscript.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep.

Competing financial interests: The authors declare no competing financial interests.
How to cite this article: Aragão-Silva, C. W. et al. The complete genome of a baculovirus isolated from an insect of medical interest: Lonemia obliqua (Lepidoptera: Saturniidae). Sci. Rep. 6, 23127; doi: 10.1038/srep23127 (2016).

This work is licensed under a Creative Commons Attribution 4.0 International License. The images or other third party material in this article are included in the article’s Creative Commons license, unless indicated otherwise in the credit line; if the material is not included under the Creative Commons license, users will need to obtain permission from the license holder to reproduce the material. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/