Classification of papillomaviruses (PVs) based on 189 PV types and proposal of taxonomic amendments

Hans-Ulrich Bernard a,⁎, Robert D. Burk b,c,d,e, Zigui Chen b, Koenraad van Doorslaer b, Harald zur Hausen f, Ethel-Michele de Villiers f

a Department of Molecular Biology and Biochemistry and Program of Public Health, University of California Irvine, Irvine, CA 92697, USA
b Department of Microbiology and Immunology, Albert Einstein College of Medicine, Bronx, New York, USA
c Department of Pediatrics, Albert Einstein College of Medicine, Bronx, New York, USA
d Department of Obstetrics, Gynecology and Women’s Health, Albert Einstein College of Medicine, Bronx, New York, USA
e Department of Epidemiology and Population Health, Albert Einstein College of Medicine, Bronx, New York, USA
f Division for the Characterization of Tumor Viruses, Deutsches Krebsforschungszentrum, Heidelberg, Germany

ARTICLE INFO

Article history:
Received 7 December 2009
Returned to author for revision 27 January 2010
Accepted 3 February 2010
Available online 5 March 2010

Keywords:
Papillomavirus
Taxonomy
Nomenclature
Family
Genus
Species
Type
Strain
Reference center

ABSTRACT

We present an expansion of the classification of the family Papillomaviridae, which now contains 29 genera formed by 189 papillomavirus (PV) types isolated from humans (120 types), non-human mammals, birds and reptiles (64, 3 and 2 types, respectively). To accommodate the number of PV genera exceeding the Greek alphabet, the prefix "dyo" is used, continuing after the Omega-PVs with Dyodelta-PVs. The current set of human PVs is contained within five genera, whereas mammalian, avian and reptile PVs are contained within 20, 3 and 1 genera, respectively. We propose standardizations to the names of a number of animal PVs. As prerequisite for a coherent nomenclature of animal PVs, we propose founding a reference center for animal PVs. We discuss that based on emerging species concepts derived from genome sequences, PV types could be promoted to the taxonomic level of species, but we do not recommend implementing this change at the current time.

© 2010 Elsevier Inc. Open access under CC BY-NC-ND license.

Introduction

Papillomaviruses (PVs) infect the epithelia of vertebrates, where they can cause neoplasias or persist asymptotically. PVs have circular double-stranded DNA genomes approximately 8 kb in size and typically contain eight genes. One of these genes, the L1, encodes the principal capsid protein and is necessary and sufficient to produce the virus-like particles used for the current vaccines. PVs have traditionally been referred to as “types”, a type being a cloned full-length PV genome, whose L1 nucleotide sequence is at least 10% dissimilar from that of any other PV type. The L1 gene is useful for classification and construction of phylogenetic trees, as it is reasonably well conserved and can be aligned for all known PVs. This allows a genome-based approach to PV nomenclature, since PVs are not amenable to classical culture techniques. This technical problem was also a reason the term “strain” was not initially employed, however, it is a taxonomic term used in the publications of the International Committee on Taxonomy of Viruses (ICTV) (Fauquet et al., 2005). Furthermore, PVs do not elicit robust antibody responses, which impeded a classification based on “serotype” designations. As a consequence, classification of PV types based predominantly on nucleotide sequence similarities with some biological and medical properties (Chan et al., 1992; van Ranst et al., 1992b; de Villiers, 1994; Myers et al., 1994; Chan et al., 1995) served as the foundation for a formal nomenclature (de Villiers et al., 2004; Fauquet et al., 2005).

PVs were designated as a distinct family, Papillomaviridae, in the 7th Report of the ICTV (van Regenmortel et al., 2002). Within the Papillomaviridae, the publication by de Villiers et al. (2004), whose authors constituted the Study Group of Papillomaviruses of the ICTV, proposed a classification of 92 human papillomavirus (HPV) and 24 animal PV types that consolidated guidelines established by the ICTV and the PV research community. This classification became formalized in the 8th Report of the International Committee on Taxonomy of Viruses (Fauquet et al., 2005). In these two publications, PVs were assigned to genera designated by Greek letters and to species within these genera according to set rules not familiar at that time.
the majority of PV researchers. The concept of what constitutes a PV species has been discussed over the years (Van Ranst et al., 1993; Chan et al., 1995), and it was a decision of the ICTV to allocate its placement in the taxonomic hierarchy of PVs (de Villiers et al., 2004; Fauquet et al., 2005), since the “type” concept is not recognized by the ICTV. The adaptation of an official nomenclature that can be utilized by PV researchers, healthcare workers, scientists and the general public requires compromise and it is the purpose of the current manuscript to expand an effective nomenclature that will serve the broad community for the near future and that is reconciled with the fixed official ICTV taxonomic structure. Table 1 compares commonly used terms referring to PV taxa with the terms de

ted by the ICTV. The table reflects an inconsistency regarding designation of species, that will be discussed later in this paper: while de Villiers et al. (2004) had given phylogenetic groups of HPVs at the level of species a name consisting of a Greek letter combined with a number, e.g. alpha-9 PV in the case HPV16 and several related HPV types, the ICTV named the “species” after one HPV type (e.g. HPV16) and considered all HPV types within that “species” as “strains”, including HPV16 (Fauquet et al., 2005).

This manuscript addresses the following objectives: (1) to update the nomenclature of genera in order to incorporate 28 novel HPV and 45 novel animal PV types that were described since 2004; (2) to refine the rules to maintain coherence of animal PV nomenclature based on the scientific name of the host species and to describe the foundation of a reference center for animal PVs; (3) to reconcile differences between some commonly used taxonomic names with terms used by the ICTV; (4) to discuss—but not to implement—a phylogenetic species concept for PVs that may lead to raising the taxonomic level of the “type” to the level of a “species”. In order to improve readability of this paper, we use the abbreviation “PV” in isolation or in the context of Greek letters, and it should be pointed out that hyphenated abbreviations like Alpha-PVs identify, strictly speaking, genera like Alphapapillomaviruses.

Results and discussion

The family Papillomaviridae

The split of the Papaviridae into two families, Papillomaviridae and Polyomaviridae was accepted by the ICTV nearly a decade ago (van Regenmortel et al., 2002). The genomes of papilloma- and polyomaviruses share only a homologous segment within the papillomavirus E1 genes and the polyomavirus T-antigens that correspond to a helix-case, suggesting an ancient common origin of the replication proteins of these viruses (Clermont and Seif, 1984; Rebrikov et al., 2002). This finding has so far no taxonomic ramifications.

Recently, two viruses of marsupials were published to contain a surprising genome organization, early genes resembling the polyomaviruses, and late genes resembling the papillomaviruses (Woolford et al., 2007; Bennett et al., 2008). These polyoma–papilloma “hybrid” viruses are not evaluated in this paper, as it seems more likely that they represent a recombination event rather than share a common ancestor and are not classified within the Papillomaviridae family.

Empir evidence of PV taxon groupings: pairwise comparisons of PV types

PV taxa are defined based on L1 nucleotide sequence identities and their topological position within PV phylogenetic trees. To evaluate the natural distribution of PV L1 identities, the L1 genes from the entire set of 189 currently characterized PVs were aligned by global multiple sequence alignment and a matrix of pairwise comparisons calculated and plotted (Fig. 1). As previously demonstrated, the distribution of L1 identities shows a bimodal pattern consistent with the genus and species nomenclature. Based on this classification, three histograms created by separate matrix analyses are displayed (Fig. 2) to evaluate the specific distribution of intraspecies, interspecies (within a genus) and intergeneric identities. (Examples: intraspecies comparison: HPV16 vs. HPV31 in the species alpha papillomavirus 9; interspecies comparison: HPV16 vs. 18, members of the species alpha papillomavirus 9 and 7, respectively; intergeneric comparison HPV16 vs. HPV41, members of the genera alpha and nu papillomavirus, respectively). Most types within a PV genus show less than 60% sequence identity to types of other genera based on global multiple sequence or pairwise alignments of the L1 genes. Nevertheless, the suggested percentage identities that define PV genera have to be taken as general, but not absolute criteria for a number of reasons. For instance, there is overlap between the intergeneric and interspecies PV identities seen at the tails of each histogram. Thus, assignment of PV types to species and genera cannot be relegated to a computer algorithm, but requires curation (i.e. interpretation based on phylogeny, genome organization, biology and pathogenicity).

Taxonomy of PVs on the level of genera

De Villiers et al. (2004) described the topology of phylogenetic trees, quantitative thresholds in nucleotide sequence comparisons and biologically distinguishing features (host species, target tissues, pathogenicity, and genome organization) that determine the classification of PVs on the level of genera. A nomenclature of these genera based on the Greek alphabet was introduced and has rapidly become accepted and widely used by the ICTV and community of PV researchers.

In 2004, sixteen groups of PVs or individual PVs fulfilled the criterion of genera, and the Greek alphabet from the letters alpha to pi was employed to create their nomenclature. Human PVs were members of five genera (Alpha-, Beta-, Gamma-, Mu- and Nu-PVs) and two genera (Eta- and Theta-PVs) were each comprised of a single bird PV. The remaining nine genera contained one or several PVs isolated from various mammals. Research over the ensuing 5 years has confirmed the notion that phylogenetic congruence of virus lineages with those of the host species is an important, although not the only mechanism of PV evolution. Consequently, search for PVs in previously understudied and remotely related host species led to the identification of PVs, whose distant relationship with one another and with all previously published PVs fulfilled the criterion to establish 13 additional genera. These include the first two PVs found in reptiles (marine turtles). All established animal PVs are listed in alphabetical order of their abbreviated name in Table 2.

The last official classification of PV genera ended with the genus Pi-PVs. The description of 13 new PV genera however, exhausts the Greek alphabet. In order to create a system that continues with the Greek alphabet, we propose to use the Greek alphabet a second time, employing the prefix “dyo”, (i.e., Greek “a second time”). In addition, we propose to omit the designations Dyolpha, Dyobeta and Dyogamma, since the Alpha-, Beta- and Gamma-PVs genera include the most common and medically important HPVs. To designate specific genera, we have followed the temporal order of publication and/or GenBank submissions of all PV nucleotide sequences and named the new genera Rho- to Omega-PV, and continued with the terms e.g., “Dyodelta-PVs”, “Dyoepsilon-PVs”. Table 3 contains a list of all PV genera and species, particularly the name of those PVs that led to the establishment of the new genera. A phylogenetic tree using the L1 nucleotide sequences of 189 PVs was generated using a Bayesian algorithm (Fig. 3) and visualizes the
relationship between all previously and newly described genera highlighting the three major genera containing the majority of HPV types.

**Nomenclature of animal PV types**

Table 2 lists the abbreviated scientific name of all animal PV types, the previously used names, the proposed phylogenetic genus, database accession numbers and references. The abbreviations have been edited to assure a coherent nomenclature of all animal PVs. Consensus within the community of papillomavirus researchers established that the name of an animal PV should be based on the scientific name of the host, using the host genus and species designation, for example FdPV1 for *Felis domesticus* PV type 1. We have applied this rule systematically, since an uncurated nomenclature of animal PVs resulted in confusion and multiple use of the same or similar abbreviations for a single type of PV. For example, a PV isolated from the European elk had been named EEPV (Ahola et al., 1986), and subsequently a different PV isolated from *Erinaceus europaeus* (hedgehog) received a similar designation, EePV (Schulz et al., 2009). Moreover, ChPV1 has been used to describe *Capra hircus* PV type 1 (van Doorslaer et al., 2006) and chimpanzee PV type 1 (van Ranst et al., 1992a). To facilitate the isolation, characterisation and publication of novel animal PVs based on a standardized evaluation and nomenclature, an Animal Papillomavirus Reference Center is proposed (see below). While this paper was compiled using publication data and database acceptance dates, deposit of the cloned viral genome will be a future requirement to recognize new animal PV names and inclusion in the official PV taxonomy, just as it has been practiced for many years in the case of human PVs.

---

**Fig. 1.** Distribution of pairwise L1 nucleotide sequence comparisons of 189 Papillomaviruses. L1 nucleotide global multiple sequence alignments were guided by amino acid alignment using MUSCLE v3.7 (Edgar, 2004) and Seaview v4.1 (Galtier et al., 1996) software. A matrix of 189 L1 regions compared to each other, resulted in a total of 17,766 identity values. Gaps were included and counted as one position. The Y-axis represents the percent of the total number of comparisons. The X-axis shows the L1 nucleotide sequence percent identity. The figure has a predominantly bimodal distribution with overlap at around 60% nucleotide sequence identity.

**Fig. 2.** Specific intergeneric, interspecies and intraspecies L1 nucleotide sequence comparisons based on the multiple sequence alignment matrix. L1 nucleotide global multiple sequence alignment was created as described in the legend to Fig. 1. The same matrix was used to evaluate the distribution of intraspecies: comparisons of PV types within the same species (161 PV types within 49 species, 558 comparisons); interspecies: comparisons of PV types within the same genus (161 PV types within 10 genera, 3207 comparisons); intergeneric: comparisons of all PV types within different genera (189 PVs in 30 genera, 14,001 comparison). The Y-axis represents the percent of the total number of comparisons. The X-axis shows the L1 nucleotide sequence percent identity.
Table 2
Alphabetical listing of the 69 known animal papillomaviruses. Designation of columns: Scient. abbrev., scientific abbreviation; prev. used abbreviation, previously used abbreviation.

<table>
<thead>
<tr>
<th>Scient. abbrev.</th>
<th>Papillomavirus name</th>
<th>Host scientific name</th>
<th>Host common name</th>
<th>Phylogeny</th>
<th>NCBI #</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>AaPV1</td>
<td>EEPV</td>
<td>Alces alces Papillomavirus 1</td>
<td>Alces Alces</td>
<td>European elk</td>
<td>Delta-1</td>
<td>M15953</td>
</tr>
<tr>
<td>BPV1</td>
<td>BPV1</td>
<td>Bos taurus Papillomavirus 1</td>
<td>Bos taurus</td>
<td>Domestic cow</td>
<td>Delta-4</td>
<td>X02346</td>
</tr>
<tr>
<td>BPV2</td>
<td>BPV2</td>
<td>Bos taurus Papillomavirus 2</td>
<td>Bos taurus</td>
<td>Domestic cow</td>
<td>Delta-4</td>
<td>M20219</td>
</tr>
<tr>
<td>BPV3</td>
<td>BPV3</td>
<td>Bos taurus Papillomavirus 3</td>
<td>Bos taurus</td>
<td>Domestic cow</td>
<td>Xi</td>
<td>AF486184</td>
</tr>
<tr>
<td>BPV4</td>
<td>BPV4</td>
<td>Bos taurus Papillomavirus 4</td>
<td>Bos taurus</td>
<td>Domestic cow</td>
<td>Xi</td>
<td>X05817</td>
</tr>
<tr>
<td>BPV5</td>
<td>BPV5</td>
<td>Bos taurus Papillomavirus 5</td>
<td>Bos taurus</td>
<td>Domestic cow</td>
<td>Epsilon</td>
<td>AF457465</td>
</tr>
<tr>
<td>BPV6</td>
<td>BPV6</td>
<td>Bos taurus Papillomavirus 6</td>
<td>Bos taurus</td>
<td>Domestic cow</td>
<td>Xi</td>
<td>AJ620208</td>
</tr>
<tr>
<td>BPV8</td>
<td>BPV8</td>
<td>Bos taurus Papillomavirus 8</td>
<td>Bos taurus</td>
<td>Domestic cow</td>
<td>Epsilon</td>
<td>DQ988913</td>
</tr>
<tr>
<td>BPV9</td>
<td>BPV9</td>
<td>Bos taurus Papillomavirus 9</td>
<td>Bos taurus</td>
<td>Domestic cow</td>
<td>Xi</td>
<td>AB331650</td>
</tr>
<tr>
<td>BPV10</td>
<td>BPV10, AA5</td>
<td>Bos taurus Papillomavirus 10</td>
<td>Bos taurus</td>
<td>Domestic cow</td>
<td>Xi</td>
<td>AB331651</td>
</tr>
<tr>
<td>CaPV1</td>
<td>RdPV1, CpPV1</td>
<td>Chelonia mydas Papillomavirus 1</td>
<td>Chelonia mydas</td>
<td>Green seaturtle</td>
<td>Dyozeta</td>
<td>EU493091</td>
</tr>
<tr>
<td>CpPV1</td>
<td>CpPV1</td>
<td>Colobus guereza Papillomavirus 1</td>
<td>Colobus guereza</td>
<td>Colobus monkey</td>
<td>Beta-1</td>
<td>EU014533</td>
</tr>
<tr>
<td>CpPV2</td>
<td>CpPV2</td>
<td>Capra hircus Papillomavirus 2</td>
<td>Capra hircus</td>
<td>Domestic goat</td>
<td>Phi</td>
<td>DQ901120</td>
</tr>
<tr>
<td>ChPV1</td>
<td>ChPV1</td>
<td>Canis familiaris Papillomavirus 7</td>
<td>Canis familiaris</td>
<td>Domestic dog</td>
<td>Tau</td>
<td>DQ901121</td>
</tr>
<tr>
<td>CmPV1</td>
<td>CmPV1</td>
<td>Canis familiaris Papillomavirus 1</td>
<td>Canis familiaris</td>
<td>Domestic dog</td>
<td>Lambda-2</td>
<td>D55633</td>
</tr>
<tr>
<td>CPV1</td>
<td>CPV1</td>
<td>Canis familiaris Papillomavirus 2</td>
<td>Canis familiaris</td>
<td>Domestic dog</td>
<td>Tau</td>
<td>AY722648</td>
</tr>
<tr>
<td>CPV2</td>
<td>CPV2, CPV1</td>
<td>Canis familiaris Papillomavirus 3</td>
<td>Canis familiaris</td>
<td>Domestic dog</td>
<td>Chi-1</td>
<td>DQ950566</td>
</tr>
<tr>
<td>CPV3</td>
<td>CPV3</td>
<td>Canis familiaris Papillomavirus 4</td>
<td>Canis familiaris</td>
<td>Domestic dog</td>
<td>Chi-2</td>
<td>EFS84537</td>
</tr>
<tr>
<td>CPV4</td>
<td>CPV4</td>
<td>Canis familiaris Papillomavirus 5</td>
<td>Canis familiaris</td>
<td>Domestic dog</td>
<td>Chi-3</td>
<td>FJ492742</td>
</tr>
<tr>
<td>CPV5</td>
<td>CPV5</td>
<td>Canis familiaris Papillomavirus 6</td>
<td>Canis familiaris</td>
<td>Domestic dog</td>
<td>Lambda-3</td>
<td>FJ492743</td>
</tr>
<tr>
<td>CPV6</td>
<td>CPV6</td>
<td>Canis familiaris Papillomavirus 7</td>
<td>Canis familiaris</td>
<td>Domestic dog</td>
<td>Tau</td>
<td>FJ492744</td>
</tr>
<tr>
<td>EcPV1</td>
<td>EcPV1</td>
<td>Equus caballus Papillomavirus 1</td>
<td>Equus ferus caballus</td>
<td>Domestic horse</td>
<td>Zeta</td>
<td>AF493323</td>
</tr>
<tr>
<td>EcPV2</td>
<td>EcPV2</td>
<td>Equus caballus Papillomavirus 2</td>
<td>Equus ferus caballus</td>
<td>Domestic horse</td>
<td>Dyozyota</td>
<td>EU031122</td>
</tr>
<tr>
<td>EdPV1</td>
<td>EdPV1</td>
<td>Erinaceus europaeus Papillomavirus 1</td>
<td>Erinaceus europaeus</td>
<td>European hedgehog</td>
<td>Dyozeta</td>
<td>FJ397923</td>
</tr>
<tr>
<td>FePV1</td>
<td>FePV1</td>
<td>Felis domesticus Papillomavirus 1</td>
<td>Felis domesticus</td>
<td>Domestic cat</td>
<td>Eta</td>
<td>AY057109</td>
</tr>
<tr>
<td>FePV2</td>
<td>FePV2</td>
<td>Felis domesticus Papillomavirus 2</td>
<td>Felis domesticus</td>
<td>Domestic cat</td>
<td>Dyozyota</td>
<td>EU759884</td>
</tr>
<tr>
<td>FIPV1</td>
<td>FIPV1</td>
<td>Francolinus leucopus Papillomavirus 1</td>
<td>Francolinus leucopus</td>
<td>Yellownecked Francolin (bird)</td>
<td>Dyopulsion</td>
<td>EU187799</td>
</tr>
<tr>
<td>LfPV1</td>
<td>LfPV1</td>
<td>Lynx rufus Papillomavirus 1</td>
<td>Lynx rufus</td>
<td>Bobcat</td>
<td>Lambda-1</td>
<td>AY904722</td>
</tr>
<tr>
<td>MaPV1</td>
<td>HaOPV</td>
<td>Mesocricetus auratus Papillomavirus 1</td>
<td>Mesocricetus auratus</td>
<td>Syrian golden hamster</td>
<td>Pi-2</td>
<td>E15111</td>
</tr>
<tr>
<td>MnPV2</td>
<td>MnPV2</td>
<td>Mastomys coucha Papillomavirus 2</td>
<td>Mastomys coucha</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>DQ664501</td>
</tr>
<tr>
<td>MnPV3</td>
<td>MnPV3</td>
<td>Macaca fascicularis Papillomavirus 1</td>
<td>Macaca fascicularis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>E029290</td>
</tr>
<tr>
<td>MnPV4</td>
<td>MnPV4</td>
<td>Macaca fascicularis Papillomavirus 2</td>
<td>Macaca fascicularis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>E029290</td>
</tr>
<tr>
<td>MnPV5</td>
<td>MnPV5</td>
<td>Macaca fascicularis Papillomavirus 3</td>
<td>Macaca fascicularis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>E029290</td>
</tr>
<tr>
<td>MnPV6</td>
<td>MnPV6</td>
<td>Macaca fascicularis Papillomavirus 4</td>
<td>Macaca fascicularis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>E029290</td>
</tr>
<tr>
<td>MnPV7</td>
<td>MnPV7</td>
<td>Macaca fascicularis Papillomavirus 5</td>
<td>Macaca fascicularis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>E029290</td>
</tr>
<tr>
<td>MnPV8</td>
<td>MnPV8, RpV-a</td>
<td>Macaca fascicularis Papillomavirus 6</td>
<td>Macaca fascicularis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>E029290</td>
</tr>
<tr>
<td>MnPV9</td>
<td>MnPV9</td>
<td>Macaca fascicularis Papillomavirus 7</td>
<td>Macaca fascicularis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>E029290</td>
</tr>
<tr>
<td>MnPV10</td>
<td>MnPV10</td>
<td>Macaca fascicularis Papillomavirus 8</td>
<td>Macaca fascicularis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>E029290</td>
</tr>
<tr>
<td>MnPV11, RpV-b</td>
<td>MnPV11, RpV-b</td>
<td>Macaca fascicularis Papillomavirus 9</td>
<td>Macaca fascicularis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>E029290</td>
</tr>
<tr>
<td>MmPV1</td>
<td>MmPV1</td>
<td>Microryzom minutus Papillomavirus 1</td>
<td>Microryzom minutus</td>
<td>Old World harvest mouse</td>
<td>Pi-1</td>
<td>DQ269468</td>
</tr>
<tr>
<td>RmPV1</td>
<td>RmPV1</td>
<td>Macaca mulata Papillomavirus 1</td>
<td>Macaca mulata</td>
<td>Rhesus macaque</td>
<td>Alpha-12</td>
<td>M60184</td>
</tr>
<tr>
<td>MmPV1</td>
<td>MmPV1, MrPV, MmPV</td>
<td>Mastomys natalensis Papillomavirus 1</td>
<td>Mastomys natalensis</td>
<td>Multimammate mouse</td>
<td>Pi-1</td>
<td>I0U1834</td>
</tr>
<tr>
<td>OaPV1</td>
<td>OaPV1</td>
<td>Ovis aries Papillomavirus 1</td>
<td>Ovis aries</td>
<td>Domestic sheep</td>
<td>Delta-3</td>
<td>U83594</td>
</tr>
<tr>
<td>OaPV2</td>
<td>OaPV2</td>
<td>Ovis aries Papillomavirus 2</td>
<td>Ovis aries</td>
<td>Domestic sheep</td>
<td>Delta-3</td>
<td>U83594</td>
</tr>
<tr>
<td>OcPV1</td>
<td>OcPV1</td>
<td>Oryctolagus cuniculus Papillomavirus 2</td>
<td>Oryctolagus cuniculus</td>
<td>Domestic sheep</td>
<td>Delta-3</td>
<td>AF227240</td>
</tr>
<tr>
<td>OpPV1</td>
<td>OpPV1</td>
<td>Odobenus rosmarus Papillomavirus 1</td>
<td>Odobenus rosmarus</td>
<td>Domestic sheep</td>
<td>Delta-3</td>
<td>U83594</td>
</tr>
<tr>
<td>PnPV1</td>
<td>PnPV1</td>
<td>Puma concolor Papillomavirus 1</td>
<td>Puma concolor</td>
<td>American White-tailed deer</td>
<td>Delta-2</td>
<td>M11910</td>
</tr>
<tr>
<td>PpPV1</td>
<td>PpPV1</td>
<td>Psittacus erithacus Papillomavirus 1</td>
<td>Psittacus erithacus</td>
<td>American White-tailed deer</td>
<td>Delta-2</td>
<td>M11910</td>
</tr>
</tbody>
</table>

(continued on next page)
To enhance a robust and workable nomenclature, we have sustained the historical use of the abbreviation “HPV” (with H standing for human or Homo, but avoiding the species designation “sapiens”) as well as “BPV” (with B standing for bovine or Bos, but avoiding the species designation “taurus”). However, the name of the cottontail rabbit PV was modified from CRPV1 to SfPV1 (for Sylvilagus floridanus), as it had been originally named SPV by one group at the Cancer Research Center in Heidelberg under the leadership of E.M. de Villiers et al. (2004) described the taxonomy of human papillomaviruses HPV1 to HPV96. Since HPV46, 55, 64 and 79 did not meet the criteria as a unique HPV type, they were omitted and their numbers left vacant (de Villiers, 2004). In addition, PV types cloned from PCR products are now accepted for full classification and the term “candidate” has been eliminated. Table 4 lists 28 HPV types (ICTV strains, see Table 1) described since 2004 and their placement within genera. Five PVs (HPV97, 102, 106, 114, and 117) belong to the Alpha-PVs, fourteen to the Gamma-PVs (HPV97, 102, 106, 114, and 117) to the Alpha-PVs, fourteen to the Gamma-PVs (HPV97, 102, 106, 114, and 117) to the Gamma-PVs (HPV97, 102, 106, 114, and 117) to the Gamma-PVs (HPV97, 102, 106, 114, and 117) to the Gamma-PVs (HPV97, 102, 106, 114, and 117) to the Gamma-PVs (HPV97, 102, 106, 114, and 117) to the Gamma-PVs. Among these nine PVs, HPV97, 98, 99, 100, 104, 105, 107, 110, 111, 113, 115, 118, 120, 122, and 124) to the Beta-PVs, and nine PVs (HPV101, 103, 108, 109, 112, 116, 119, 121, and 123) to the Gamma-PVs. Among these nine PVs, HPV101, 103, and 108 diverge convincingly from all other HPV types in that they lack an E6 ORF (Chen et al., 2007a; Nobre et al., 2009). In spite of this distinction, these three types are included in the genus Gamma-PV based on the present rules of sequence similarities in the L1 ORF and the resulting topology of the phylogenetic tree.

### Subtypes and variants of PV types

The definition and properties of PV subtypes and variants as DNA isolates with less than 10% sequence diversity in the L1 gene have been discussed (de Villiers et al., 2004; Calleja-Macias et al., 2005; Bernard et al., 2006). These issues are not further addressed here, as the ICTV does not implement taxonomic systems below the species level. A nomenclature of variants of Alpha-PV types associated with cervix cancer, which will be based on complete genome sequences and extending beyond the historic classification of HPV16 and 18 variant lineages that were based on geographic association (Bernard et al., 2006), is being developed by some of us (Burk et al., in prep.).

### Reference centers for human and animal papillomaviruses

The Reference Center for Human Papillomaviruses at the German Cancer Research Center in Heidelberg under the leadership of E.M. de Villiers has for the past 25 years been instrumental in confirming the nucleotide sequence of novel HPV types, assigning the appropriate HPV numbers, depositing and maintaining reference samples, and, if permitted by proprietary rules, distributing DNA samples. This process has been essential to assure an orderly expansion of HPV types and avoid misinterpretation of incomplete or heterologous DNA clones and isolates not meeting the established criteria. The continued maintenance of this reference center and service to the community is of great importance.

In order to avoid misclassifications and maintain a unique nomenclature, we have made efforts to support the establishment of a Repository for Animal Papillomaviruses since no similar reference center for animal PVs has yet been established. One of us (R.D.B.) in collaboration with Dr. Rob DeSalle of the Sackler Institute for Comparative Genomics at the American Museum for Natural History will facilitate the creation of this service. The function of such a center for animal PVs will be to (i) streamline the curation of non-human PVs, (ii) establish a repository for all characterized non-human PVs, and (iii) establish a reference center for all non-human PVs by obtaining the cloned genomes and re-sequencing the provided clones to confirm the existence of each novel non-human PV. As curation of novel HPV types has been necessary for the orderly HPV nomenclature, this repository will implement a similar system for animal PVs, where, prior to publication of a novel animal PV, an “official name” has been designated and the cloned genome been publicly deposited.

### Table 2 (continued)

<table>
<thead>
<tr>
<th>Scient. abbrev.</th>
<th>Prev. used abbreviation</th>
<th>Papillomavirus name</th>
<th>Host scientific name</th>
<th>Phylogeny</th>
<th>NCBI #</th>
<th>Reference (in direct submission)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PippPV1</td>
<td>PippPV1</td>
<td>Pantera leo persica Papillomavirus 1</td>
<td>Panthera leo persica</td>
<td>Asiatic lion</td>
<td>Lambda-1 AS020742</td>
<td>Rector et al. (2007)</td>
</tr>
<tr>
<td>PippPV1</td>
<td>PippPV1</td>
<td>Procyon lotor Papillomavirus 1</td>
<td>Procyon lotor</td>
<td>Raccoon</td>
<td>Lambda-4 ASY67115</td>
<td>Rector et al. (2005b)</td>
</tr>
<tr>
<td>PippPV1</td>
<td>PippPV1, PCPV</td>
<td>Pan paniscus Papillomavirus 1</td>
<td>Pan paniscus</td>
<td>Pygmy chimpanzee</td>
<td>Alpha-10 X52844</td>
<td>Van Ranst et al. (1991)</td>
</tr>
<tr>
<td>PrPV1</td>
<td>PrPV1</td>
<td>Phocoena spinippinnis Papillomavirus 1</td>
<td>Phocoena spinippinnis</td>
<td>Burmeister’s porpoise</td>
<td>Omikron AJ238373</td>
<td>Cassonnet et al. (2007)</td>
</tr>
<tr>
<td>RaPV1</td>
<td>RaPV1</td>
<td>Rousettus aegypticus Papillomavirus 1</td>
<td>Rousettus aegypticus</td>
<td>Egyptian rousette</td>
<td>Psi DQ366842</td>
<td>Rector et al. (2006)</td>
</tr>
<tr>
<td>RnPV1</td>
<td>RnPV1</td>
<td>Rattus norvegicus Papillomavirus 1</td>
<td>Rattus norvegicus</td>
<td>Norwegian rat</td>
<td>Pi-1 GQ180114</td>
<td>Schultz et al. (2009)</td>
</tr>
<tr>
<td>RifPV1</td>
<td>RifPV, RVF</td>
<td>Rangifer tarandus Papillomavirus 1</td>
<td>Rangifer tarandus</td>
<td>Reindeer</td>
<td>Delta-1 AF443292</td>
<td>Moreno-Lopez et al. (1987)</td>
</tr>
<tr>
<td>SPPV1</td>
<td>SPPV1</td>
<td>Sylvilagus floridanus Papillomavirus 1</td>
<td>Sylvilagus floridanus</td>
<td>Cottontail rabbit</td>
<td>Kappa-2 K02708</td>
<td>Stevens et al. (2008)</td>
</tr>
<tr>
<td>SnPV1</td>
<td>SnPV1</td>
<td>Sus scrofa Papillomavirus 1</td>
<td>Sus scrofa</td>
<td>Domestic pig</td>
<td>Dyodelta EF395818</td>
<td>Rector et al. (2004)</td>
</tr>
<tr>
<td>TmPV1</td>
<td>TmPV1</td>
<td>Trichgeus manatus latrostris Papillomavirus 1</td>
<td>Trichgeus manatus latrostris</td>
<td>Caribbean manatee</td>
<td>Rino AY609301</td>
<td>Rector et al. (2004)</td>
</tr>
<tr>
<td>TIPV1</td>
<td>TIPV1</td>
<td>Tursios truncatus Papillomavirus 1</td>
<td>Tursios truncatus</td>
<td>Bottlenosed dolphin</td>
<td>Upsilon-1 EU240894</td>
<td>Rector et al. (2008)</td>
</tr>
<tr>
<td>TIPV2</td>
<td>TIPV2</td>
<td>Tursios truncatus Papillomavirus 2</td>
<td>Tursios truncatus</td>
<td>Bottlenosed dolphin</td>
<td>Upsilon-2 AY956402</td>
<td>Rehanz et al. (2006)</td>
</tr>
<tr>
<td>TIPV3</td>
<td>TIPV3</td>
<td>Tursios truncatus Papillomavirus 3</td>
<td>Tursios truncatus</td>
<td>Bottlenosed dolphin</td>
<td>Upsilon-1 EU240895</td>
<td>Rector et al. (2008)</td>
</tr>
<tr>
<td>UmPV1</td>
<td>UmPV1</td>
<td>Ursus maritimus Papillomavirus 1</td>
<td>Ursus maritimus</td>
<td>Polar bear</td>
<td>Omega EF536349</td>
<td>Stevens et al. (2008a)</td>
</tr>
<tr>
<td>UuPV1</td>
<td>UuPV1</td>
<td>Uncia uncia Papillomavirus 1</td>
<td>Uncia uncia</td>
<td>Snow leopard</td>
<td>Lambda-1 DQ180484</td>
<td>Rector et al. (2007)</td>
</tr>
</tbody>
</table>

See Supplemental table for ICTV animal papillomavirus nomenclature.
Table 3
Papillomavirus genera and species.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species (common use)</th>
<th>Species (ICTV)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alphapapillomavirus</strong></td>
<td>Alpha-1</td>
<td>Human Papillomavirus 32</td>
</tr>
<tr>
<td>Alpha-2</td>
<td>Human Papillomavirus 10</td>
<td></td>
</tr>
<tr>
<td>Alpha-3</td>
<td>Human Papillomavirus 61</td>
<td></td>
</tr>
<tr>
<td>Alpha-4</td>
<td>Human Papillomavirus 2</td>
<td></td>
</tr>
<tr>
<td>Alpha-5</td>
<td>Human Papillomavirus 26</td>
<td></td>
</tr>
<tr>
<td>Alpha-6</td>
<td>Human Papillomavirus 53</td>
<td></td>
</tr>
<tr>
<td>Alpha-7</td>
<td>Human Papillomavirus 18</td>
<td></td>
</tr>
<tr>
<td>Alpha-8</td>
<td>Human Papillomavirus 7</td>
<td></td>
</tr>
<tr>
<td>Alpha-9</td>
<td>Human Papillomavirus 16</td>
<td></td>
</tr>
<tr>
<td>Alpha-10</td>
<td>Human Papillomavirus 6</td>
<td></td>
</tr>
<tr>
<td>Alpha-11</td>
<td>Human Papillomavirus 34</td>
<td></td>
</tr>
<tr>
<td>Alpha-12</td>
<td>Macaca mulata Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Alpha-13</td>
<td>Human Papillomavirus 54</td>
<td></td>
</tr>
<tr>
<td>Alpha-14</td>
<td>Human Papillomavirus 90</td>
<td></td>
</tr>
<tr>
<td>Alpha-15</td>
<td>Human Papillomavirus 8</td>
<td></td>
</tr>
<tr>
<td>Alpha-16</td>
<td>Human Papillomavirus 92</td>
<td></td>
</tr>
<tr>
<td>Alpha-17</td>
<td>Human Papillomavirus 96</td>
<td></td>
</tr>
<tr>
<td>Alpha-18</td>
<td>Macaca fascicularis Papillomavirus 2</td>
<td></td>
</tr>
<tr>
<td><strong>Betapapillomavirus</strong></td>
<td>Beta-1</td>
<td>Alces alces Papillomavirus 1</td>
</tr>
<tr>
<td>Beta-2</td>
<td>Odocolus virginianus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Beta-3</td>
<td>Ovis aries Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Beta-4</td>
<td>Bos taurus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Beta-5</td>
<td>Capreolus capreolus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Epsilon-1</td>
<td>Mouse Papillomavirus 5</td>
<td></td>
</tr>
<tr>
<td>Zetapapillomavirus</td>
<td>Zeta-1</td>
<td>Equus caballus Papillomavirus 1</td>
</tr>
<tr>
<td>Eta-1</td>
<td>Fringilla coelebs Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Kappa-1</td>
<td>Oryctolagus cuniculus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Kappa-2</td>
<td>Sylvilagus floridanus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Lambda-1</td>
<td>Felis domesticus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Lambda-2</td>
<td>Canis familiaris Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Lambda-3</td>
<td>Canis familiaris Papillomavirus 6</td>
<td></td>
</tr>
<tr>
<td>Lambda-4</td>
<td>Procyon lotor Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Mu-1</td>
<td>Human Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Mu-2</td>
<td>Human Papillomavirus 63</td>
<td></td>
</tr>
<tr>
<td>Nu-1</td>
<td>Human papillomavirus 41</td>
<td></td>
</tr>
<tr>
<td>Xi-1</td>
<td>Bos taurus Papillomavirus 3</td>
<td></td>
</tr>
<tr>
<td>Pi-1</td>
<td>Mesocricetus auratus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Pi-2</td>
<td>Micromys minutus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Rho-1</td>
<td>Triches chus manatus latrostris Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Sigma-1</td>
<td>Eretizon duratum Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Tau-1</td>
<td>Canis familiaris Papillomavirus 2</td>
<td></td>
</tr>
<tr>
<td>Upsilon-1</td>
<td>Tursiops truncatus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Upsilon-2</td>
<td>Tursiops truncatus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Phi-1</td>
<td>Capra hircus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Chi-1</td>
<td>Canis familiaris Papillomavirus 3</td>
<td></td>
</tr>
<tr>
<td>Chi-2</td>
<td>Canis familiaris Papillomavirus 4</td>
<td></td>
</tr>
<tr>
<td>Psi-1</td>
<td>Roussetia aegyptiacus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Omega-1</td>
<td>Ursus maritimus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Dyo-1</td>
<td>Sus scrofa Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Dyo-2</td>
<td>Francolinus leucopus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Dyo-3</td>
<td>Caretta caretta Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Dyo-4</td>
<td>Erinaceus europaeus Papillomavirus 1</td>
<td></td>
</tr>
<tr>
<td>Phy-1</td>
<td>Felis domesticus Papillomavirus 2</td>
<td></td>
</tr>
<tr>
<td>Tri-1</td>
<td>Equus caballus Papillomavirus 2</td>
<td></td>
</tr>
</tbody>
</table>

Phylogenetic and biological considerations regarding the nature of “PV species” and “PV types”

Defining PV taxa below the level of genera resulted in some inconsistencies between the official ICTV PV nomenclature (Fauquet et al., 2005) and that used by the scientific community (de Villiers et al., 2004). A goal of the current Study Group of Papillomaviruses is to harmonize the official ICTV designations with the known genetics and biology of PVs. The ICTV only names species after a specific virus, such as HPV16, and related types including the “type-species” are designated as strains within the species (see Table 1) (Fauquet et al., 2005). For example, the commonly used term “PV species Alpha-9” (de Villiers et al., 2004) is a synonym for what the ICTV called the “HPV16 species”, which contains the HPV types (strains) 16, 31, 35, 33, 52, 58 and 67. Although it can be argued (see below) that a PV “type” has many characteristics of a “species”, we recommend maintaining the current allocation of the taxonomic levels of genus and species. Nevertheless, since the species designations of de Villiers et al. (2004) have been widely accepted and useful to the scientific community, we support their continued use.

The ICTV proposed guidelines defining that a species should be “a polythetic class of viruses that constitute a replicating lineage and occupies a particular ecological niche” (van Regenmortel et al., 1991). The term “polythetic” means that several or all possible criteria or attributes be used to determine a viral species. This definition suggests that a single property, even genomic sequences, might be insufficient to define a viral species. This definition has been challenged (van Regenmortel et al., 2000; Drebot et al., 2002; Gibbs and Gibbs, 2006). Concepts of defining viral species have always been complicated and are not yet mature. Among several complimentary approaches, nucleotide sequence-based comparisons developed in the last few decades have impacted taxonomic research throughout biology, led to completely new insights into the species concept, and have become widely accepted as a solid taxonomic criterion. Papillomaviruses were the first viruses to be significantly classified by comparison of viral genomes, in part, because of the lack of a culture or serologic system.

The age of PV types is a major component of equating PV types with PV species (Rector et al., 2007). Even closely related PV types have evolved over time scales equivalent to those that gave rise to their host species, i.e. over millions of years. This is fundamentally different from the emergence of quasi-species of RNA viruses over very short periods of time, such as the human immunodeficiency viruses (Rambaut et al., 2004), or from human rhinoviruses that have rapidly evolved in the relatively short time span since the origin of humans (Palmenberg et al., 2009). In addition, the distribution of PV type identities within a species (intraspecies identity) as shown in Figs. 1 and 2 has a normal distribution suggestive of a natural taxonomic order. Moreover, reports of phenotypic idiosyncrasies of closely related PV types, classified within a single species, continue to accumulate. Some notable examples are found among the members of the Alpha-PV 10 species (species HPV6 and related “strains” in ICTV nomenclature). For example, HPV6 and 11 show significantly different tissue tropism, HPV6 being more common in genital warts, HPV11 more common in laryngeal papillomas. The closely related type, HPV13, causes focal epithelial hyperplasia of the oral cavity and has neither been found in genital warts nor in laryngeal papillomas (de Villiers, 1994, 2001). HPV16, 31 and 35 are grouped in the species Alpha-PV 9 (species HPV16 and related “strains” in ICTV nomenclature). The association between HPV16 and cancer is significantly stronger than that between either HPV31 or HPV35 (Munoz et al., 2003). HPV16 is uniquely associated with tumors of the oropharyngeal region.

In summary, we presented arguments on how a phylogenetic species concept could be applied to PV taxonomy. This concept has increasing impact throughout biology, but is presently not implemented in virology, and we therefore do not yet recommend implementation at this point. Once widely accepted, a phylogenetic species concept would
lead to a promotion of PV types (strains) to species, and of the present species to sub-genera, while genera would remain unchanged.

Online papillomavirus database

PV nucleotide sequences are deposited in the GenBank and EMBL nucleotide sequence databases. A compilation of all sequences available in the mid-1990s, was compiled and reviewed in the "Papillomavirus Database" sponsored by NIAID and published online and as hardcopy by the Los Alamos National Laboratory (Myers et al., 1994). A new interactive database "Papillomavirus Episteme" (http://pave.niaid.nih.gov/#home) is currently under development.

Materials and methods

Origin of sequences

This paper is based on published PV sequences, which can be accessed either through the listed references, or the GenBank accession numbers in the Tables 2 and 4.

Acknowledgments

This paper was written by four authors that form the PV Study Group of the ICTV appointed in 2009 (H.U.B., R.D.B., H.Z.H., and E.M.deV.) and two colleagues (Z.C. and K.V.D.). We thank Ignacio G. Bravo and Benjamin Smith for stimulating discussions. RDB is support in part by Public Health Service awards CA78527 from the National Cancer Institute (RDB) and center grants to the Einstein Cancer Research Center and the Center for AIDS Research (CFAR).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.virol.2010.02.002.

References


Fig. 3. Phylogenetic tree inferred from the L1 nucleotide sequences of 189 papillomaviruses. The phylogeny analysis is based on the multiple L1 nucleotide sequence alignment of 189 PV types that was used in Figs. 1 and 2. MrBayes v3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) with 10,000,000 cycles for the Markov chain Monte Carlo (MCMC) algorithm was used to generate a phylogenetic tree. For Bayesian tree construction, the computer program ModelTest v3.7 (Posada and Crandall, 1998) identified the best evolutionary model. The identified gamma model was set for among-site rate variation and allowed all substitution rates of aligned sequence to be different.

Table 4

Human papillomaviruses characterized since 2004.

<table>
<thead>
<tr>
<th>HPV type</th>
<th>PV genus</th>
<th>PV species (common use)</th>
<th>PV species (ICTV)</th>
<th>GenBank No.</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>HPV 97</td>
<td>Alphapapillomavirus</td>
<td>Alpha-7</td>
<td>Human Papillomavirus 18</td>
<td>DQ890080</td>
<td>Chen et al. (2007a)</td>
</tr>
<tr>
<td>HPV 98</td>
<td>Betapapillomavirus</td>
<td>Beta-1</td>
<td>Human Papillomavirus 5</td>
<td>FM955837</td>
<td>de Villiers and Gunst (2009)</td>
</tr>
<tr>
<td>HPV 99</td>
<td>Betapapillomavirus</td>
<td>Beta-1</td>
<td>Human Papillomavirus 5</td>
<td>FM955838</td>
<td>de Villiers and Gunst (2009)</td>
</tr>
<tr>
<td>HPV 100</td>
<td>Betapapillomavirus</td>
<td>Beta-2</td>
<td>Human Papillomavirus 9</td>
<td>FM955839</td>
<td>de Villiers and Gunst (2009)</td>
</tr>
<tr>
<td>HPV 101</td>
<td>Gammapapillomavirus</td>
<td>Gamma-6</td>
<td>Human Papillomavirus 101</td>
<td>NC_008189</td>
<td>Chen et al. (2007c)</td>
</tr>
<tr>
<td>HPV 102</td>
<td>Alphapapillomavirus</td>
<td>Alpha-3</td>
<td>Human Papillomavirus 61</td>
<td>DQ800883</td>
<td>Chen et al. (2007b)</td>
</tr>
<tr>
<td>HPV 103</td>
<td>Gammapapillomavirus</td>
<td>Gamma-6</td>
<td>Human Papillomavirus 101</td>
<td>NC_008188</td>
<td>Chen et al. (2007c)</td>
</tr>
<tr>
<td>HPV 104</td>
<td>Betapapillomavirus</td>
<td>Beta-2</td>
<td>Human Papillomavirus 9</td>
<td>FM955840</td>
<td>de Villiers and Gunst (2009)</td>
</tr>
<tr>
<td>HPV 105</td>
<td>Betapapillomavirus</td>
<td>Beta-1</td>
<td>Human Papillomavirus 5</td>
<td>FM955841</td>
<td>de Villiers and Gunst (2009)</td>
</tr>
<tr>
<td>HPV 106</td>
<td>Alphapapillomavirus</td>
<td>Alpha-14</td>
<td>Human Papillomavirus 90</td>
<td>DQ800882</td>
<td>Chen et al. (2007b)</td>
</tr>
<tr>
<td>HPV 107</td>
<td>Betapapillomavirus</td>
<td>Beta-2</td>
<td>Human Papillomavirus 9</td>
<td>EU422223</td>
<td>Vasiljevic et al. (2008)</td>
</tr>
<tr>
<td>HPV 108</td>
<td>Gammapapillomavirus</td>
<td>Gamma-6</td>
<td>Human Papillomavirus 101</td>
<td>NC_012213</td>
<td>Nobre et al. (2009)</td>
</tr>
<tr>
<td>HPV 109</td>
<td>Gammapapillomavirus</td>
<td>Gamma-7</td>
<td>Human Papillomavirus 9</td>
<td>NC_012485</td>
<td>Ekstrom et al. (in press)</td>
</tr>
<tr>
<td>HPV 110</td>
<td>Betapapillomavirus</td>
<td>Beta-2</td>
<td>Human Papillomavirus 9</td>
<td>EU140348</td>
<td>Vasiljevic et al. (2008)</td>
</tr>
<tr>
<td>HPV 111</td>
<td>Betapapillomavirus</td>
<td>Beta-2</td>
<td>Human Papillomavirus 9</td>
<td>EU140349</td>
<td>Vasiljevic et al. (2008)</td>
</tr>
<tr>
<td>HPV 112</td>
<td>Gammapapillomavirus</td>
<td>Gamma-8</td>
<td>Human Papillomavirus 112</td>
<td>EU140442</td>
<td>Ekstrom et al. (in press)</td>
</tr>
<tr>
<td>HPV 113</td>
<td>Betapapillomavirus</td>
<td>Beta-2</td>
<td>Human Papillomavirus 9</td>
<td>FM955842</td>
<td>de Villiers and Gunst (2009)</td>
</tr>
<tr>
<td>HPV 114</td>
<td>Alphapapillomavirus</td>
<td>Alpha-3</td>
<td>Human Papillomavirus 61</td>
<td>GQ244465</td>
<td>Ekstrom et al. (in press)</td>
</tr>
<tr>
<td>HPV 115</td>
<td>Betapapillomavirus</td>
<td>Beta-3</td>
<td>Human Papillomavirus 49</td>
<td>FJ947080</td>
<td>Chouhy et al. (2010)</td>
</tr>
<tr>
<td>HPV 116</td>
<td>Gammapapillomavirus</td>
<td>Gamma-9</td>
<td>Human Papillomavirus 116</td>
<td>FJ804072</td>
<td>Li et al. (2009)</td>
</tr>
<tr>
<td>HPV 117</td>
<td>Alphapapillomavirus</td>
<td>Alpha-2</td>
<td>Human Papillomavirus 10</td>
<td>GQ246950</td>
<td>Köhler et al. (in press)</td>
</tr>
<tr>
<td>HPV 118</td>
<td>Betapapillomavirus</td>
<td>Beta-1</td>
<td>Human Papillomavirus 5</td>
<td>GQ246951</td>
<td>Chen et al. unpubl.</td>
</tr>
<tr>
<td>HPV 119</td>
<td>Gammapapillomavirus</td>
<td>Gamma-8</td>
<td>Human Papillomavirus 12</td>
<td>GQ845441</td>
<td>Chen et al. unpubl.</td>
</tr>
<tr>
<td>HPV 120</td>
<td>Betapapillomavirus</td>
<td>Beta-2</td>
<td>Human Papillomavirus 9</td>
<td>GQ845442</td>
<td>Chen et al. unpubl.</td>
</tr>
<tr>
<td>HPV 121</td>
<td>Gammapapillomavirus</td>
<td>Gamma-10</td>
<td>Human Papillomavirus 121</td>
<td>GQ845443</td>
<td>Chen et al. unpubl.</td>
</tr>
<tr>
<td>HPV 122</td>
<td>Betapapillomavirus</td>
<td>Beta-2</td>
<td>Human Papillomavirus 9</td>
<td>GQ845444</td>
<td>Chen et al. unpubl.</td>
</tr>
<tr>
<td>HPV 123</td>
<td>Gammapapillomavirus</td>
<td>Gamma-7</td>
<td>Human Papillomavirus 109</td>
<td>GQ845445</td>
<td>Chen et al. unpubl.</td>
</tr>
<tr>
<td>HPV 124</td>
<td>Betapapillomavirus</td>
<td>Beta-1</td>
<td>Human Papillomavirus 5</td>
<td>GQ845446</td>
<td>Chen et al. unpubl.</td>
</tr>
</tbody>
</table>

This content is provided for educational purposes and may not be comprehensive or up-to-date. Always verify the information through official sources.


