Predominant genotypes of human papillomavirus in Korean men

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Abstract

Human papillomavirus (HPV) is associated with several types of cancers in men, including head and neck, anal and genital cancers. However, research on HPV has primarily focused on women, and available data from men are limited. This study aimed to evaluate the positivity rate, genotype distribution, and co-infection rates of HPV in Korean men who visited a hospital owing to a suspected sexually transmitted infection. A total of 14,994 samples sent to specialized laboratories between January 2020 and June 2023 were included in this study. HPV genotypes were determined in the collected specimens (including swabs and urine, semen and prostatic fluid samples). The HPV genotypes varied with age; single infections and co-infections with two or more genotypes were confirmed. A high positivity rate of HPV was observed among Korean men from their teens to their 70s. Single and co-infection positivity rates differed significantly among ages (χ² = 81.502, p < 0.0001). The most frequently identified HPV genotypes were 6 and 11, whereas the positivity rate of the high-risk genotype 16 increased with age (χ² = 1012.028, p < 0.0001). Sexual health management efforts should be directed toward both men and women to mitigate disease burden and transmission risks and prevent cervical cancer. A comprehensive analysis of HPV infections in men is warranted.

Keywords

Cervical cancer; Genotype; Human papillomavirus; Male; Multiple infection

1. Introduction

Human papillomavirus (HPV) is the leading cause of cervical cancer and caused the death of more than 340,000 women worldwide in 2020 according to data from the World Health Organization. The management and treatment of cervical cancer are costly, and certain HPV genotypes (including genotypes 16 and 18) are associated with a high risk of developing the disease [1, 2]. In addition, HPV has been linked with other cancers, including head and neck, anal, male genital and prostate cancers. Although HPV-related cervical cancer in women has been extensively researched, interest in HPV infections in men has only recently begun to increase [3–5].

Previous studies on HPV infection in men have primarily focused on younger age groups that are commonly sexually active [6]. These studies have reported positivity rates, infection symptoms, vaccination awareness and barriers and knowledge gaps. However, research in healthy male populations of various ethnicities is still limited, and existing studies have reported inconsistent results. This gap in research regarding HPV infection in men contrasts with the relatively extensive literature addressing the diagnosis, treatment and prevention in women [6, 7].

Because HPV infection in men can affect women, research on reducing the transmission of HPV-related diseases by focusing on the role of men is imperative [8, 9]. Studies and efforts aimed at preventing HPV infection in men can contribute to understanding sex differences and play a role in reducing health inequalities and sex-based medical biases [10, 11]. Disseminating information and preventive measures for HPV-related diseases to both men and women will contribute to building healthier societies.

Many countries have implemented vaccination programs, but disease progression and treatment may differ according to specific HPV genotypes [12]. Therefore, evaluating the positivity rate of different HPV genotypes in the general male population is crucial. However, large amounts of data on HPV infection are required. In this study, we investigated HPV infection rates in men using a high-throughput HPV monitoring initiative, representing a large-scale research effort.

The primary objective of this study was to evaluate the positivity rates, circulating genotypes, and co-infection rates of HPV in Korean men who visited a hospital owing to a suspected sexually transmitted infection (STI). This study aimed to provide foundational data for the development of specialized treatment and prevention strategies targeting HPV strains with specific genotypes that predominantly infect men.
2. Materials and methods

2.1 Study design and methods

Men who had been referred to an outsourced testing center (U2Bio) for HPV testing at hospitals nationwide (including primary hospitals with 30 or fewer beds, secondary hospitals with 30–300 beds, and tertiary hospitals with more than 300 beds) between January 2020 and June 2023 were included. They mainly visited the hospital owing to suspected STIs. All personal information except sex and age was removed, and only test result data were collected. After sample collection, deoxyribonucleic acid (DNA) extraction and multiplex real-time polymerase chain reaction (RT-PCR) were conducted to identify HPV genotypes. All testing procedures adhered to the manufacturer’s protocol.

Swabs and tissue, urine and other samples, including semen and prostatic fluid, were collected. No data were collected regarding the anatomical site of swab collection. Swabs were collected by rubbing a sterile cotton swab on the affected area. Tissue was obtained by biopsy, and urine was collected once. DNA was extracted from samples within 48 h using QIAseq™-HPV kit (SP type, Qiagen, Hilden, Germany) and refrigerated at 4 °C until testing. The OmniPlex™-HPV kit (GM 3300, Genematrix, Seongnam, Korea) with a CFX96 real-time thermocycler (Bio-Rad, Hercules, CA, USA) was used to perform RT-PCR. The reaction mixture included 2.5 mM deoxynucleotide triphosphates (5 µL), 10× reaction buffer (5 µL), primer mixture (20 pmol), Taq polymerase (0.5 µL), and distilled water adjusted to a final volume of 40 µL. Subsequently, 10 µL of each sample was added to the mixture immediately before the reaction. The PCR conditions involved denaturation at 94 °C for 1 min, annealing at 51 °C for 1 min, and extension at 72 °C for 1 min, repeated for 35 cycles. Finally, extension was carried out at 72 °C for 10 min. HPV genotypes were identified based on the methods employed. The following 41 HPV genotypes could be identified: 6, 11, 16, 18, 26, 30, 31, 32, 33, 35, 39, 40, 42, 43, 44, 45, 51, 52, 53, 54, 55, 56, 58, 59, 61, 62, 66, 67, 68, 69, 70, 71, 72, 73, 74, 81, 82, 83, 84, 87 and 99. Twelve HPV genotypes (16, 18, 31, 33, 35, 39, 45, 51, 52, 56, 58 and 59) were classified as being high risk and 29 (6, 11, 26, 30, 32, 40, 42, 43, 44, 53, 54, 55, 61, 62, 66, 67, 68, 69, 70, 71, 72, 73, 74, 81, 82, 83, 84, 87 and 99) as being low risk. The HPV positivity rate in this study was defined as the presence of at least one positive result among the 41 HPV genotypes, irrespective of the specific genotype detected.

2.2 Procedure

The sample selection process for data collection is illustrated in Fig. 1. Of the 32,565 HPV specimens tested between January 2020 and June 2023, we excluded cases with insufficient information on sex (n = 417) or age (n = 194), those with data entry errors in age (n = 79), those without a personal identification number (n = 85), and those with a missing HPV

![Diagram](https://via.placeholder.com/150)
genotype (n = 1).

The study was restricted to samples from adult men and excluded samples from women (n = 16,795). The total number of samples included in this study was 14,994.

### 2.3 Data analysis

All statistical analyses were performed using SAS software (version 9.4, SAS Institute, Cary, NC, USA), Excel for Microsoft 365 MSO (version 2308, Microsoft, Redmond, WA, USA), and RStudio (version 2023.06.1, Posit, PBC, Boston, MA, USA). Nominal data such as HPV positivity rates are presented as frequencies and percentages, and differences in positivity rates were analyzed using the chi-squared test. Continuous data such as age are presented as means and standard deviations. Differences in means were analyzed by one-way analysis of variance. Statistical significance was set at \( p \)-values < 0.05.

### 3. Results

#### 3.1 Number of HPV infections and testing types

The infection rate was 62.9%, with the remaining 37.1% of patients not presenting evidence of infection. The maximum number of simultaneous co-infections was 10, reported in one person. The majority of samples (57.6%) exhibited single-type infection. Dual-type co-infections accounted for 25.1% of the positive samples; co-infections with three genotypes, for 10.9%; and co-infections with four or more genotypes, for 6.3%. Tissue samples and swabs accounted for the majority of the samples (Table 1).

#### 3.2 Positivity rates for HPV infection according to age

Table 2 illustrates age-specific positivity rates for HPV infection by specimen. The overall HPV positivity rate was 62.9%, consistently exceeding 50% across all age groups. The highest positivity rate was observed in individuals in their 50s (69.6%), whereas the lowest was observed in teenagers (54.5%). For almost all age groups (except individuals in their 70s), single infections were significantly more common than co-infections \( (\chi^2 = 81.502, p < 0.0001) \).

Among the specimens, the highest positivity rate for swabs was in the group of men in their 50s (62.6%), while the lowest was in the group of men 19 years old and younger (42.7%). The group with the highest number of single infections was men in their 60s (69.1%), and the highest number of multiple infections was seen in the group of men in their 70s and older (66.7%). For tissues, the highest positivity rate was among those aged 19 years and younger (94.6%), while the lowest positivity rate was among those aged 70 years and older (77.8%). For urine, the highest positivity rate was among those aged 19 years and younger (28.6%), and the lowest was among those aged 70 years and older (0%), but this group only had two specimens.

#### 3.3 Rates of single and multiple HPV infections

Rates of single and multiple HPV infections in men were 57.6% and 42.4%, respectively. When examining multiple HPV infections in men across all age groups, the highest rate was found in men aged \( \geq 70 \) years (13, 68.4%), although the sample size was limited.

#### 3.4 Age-specific HPV co-infections

Examining age-specific concurrent HPV infections in men revealed that dual infections with two viruses were most prevalent in those in their 30s, whereas infections with three or more viruses concurrently were most common in individuals aged \( \geq 70 \) years.

#### 3.5 Genotypes and average ages of HPV-positive men

The mean age of HPV-positive men was 33.3 years, with a standard deviation of \( \pm 9.0 \) years. Fig. 2 presents the genotypes and average ages of HPV-positive Korean men. Excluding the age of individuals infected with genotype 69 (45.3 ± 15.5 years), the average age of individuals infected with HPV ranged from 30.4 ± 7.9 years (type 18, high risk) to 37.6 ± 11.0 years (type 32). The highest mean age corresponded to individuals infected with genotype 69 \( (F = 7.38, p < 0.0001) \). Further details of each specimen are provided in Supplementary Table 1, which shows the mean age of HPV-positive men by genotype and specimen. For swabs, patients with genotype 69 had the highest mean age (45.9 ± 0.0 years). For tissue samples, patients with genotype 32 had the highest mean age (36.9 ± 9.3 years), and for urine samples, patients with genotype 54 had the highest mean age (48.0 ± 18.7 years).

### Table 1. Rate of concurrent HPV infections and positivity rate in Korean men (N = 14,994).

<table>
<thead>
<tr>
<th>Category</th>
<th>n</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Negative</td>
<td>5566</td>
<td>37.1</td>
</tr>
<tr>
<td>Positive</td>
<td>9428</td>
<td>62.9</td>
</tr>
<tr>
<td>Concurrent infection</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Single</td>
<td>5427</td>
<td>57.7</td>
</tr>
<tr>
<td>Double</td>
<td>2371</td>
<td>25.1</td>
</tr>
<tr>
<td>Triple</td>
<td>1032</td>
<td>10.9</td>
</tr>
<tr>
<td>≥Quadruple</td>
<td>598</td>
<td>6.3</td>
</tr>
<tr>
<td>Specimen</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Swab</td>
<td>5095</td>
<td>54.0</td>
</tr>
<tr>
<td>Tissue</td>
<td>3744</td>
<td>39.7</td>
</tr>
<tr>
<td>Urine</td>
<td>156</td>
<td>1.7</td>
</tr>
<tr>
<td>Others</td>
<td>433</td>
<td>4.6</td>
</tr>
</tbody>
</table>

* N, total number of participants; n, number of cases in the category; Others, semen, prostatic fluid.*
### TABLE 2. Age-specific positivity rates and co-infection rates by specimen (N = 9428).

<table>
<thead>
<tr>
<th>Anatomic site</th>
<th>Single</th>
<th>≥Double</th>
<th>Double</th>
<th>Triple</th>
<th>≥Quadruple</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age group (yr)</td>
<td>n</td>
<td>%</td>
<td>n</td>
<td>%</td>
<td>n</td>
</tr>
<tr>
<td>Total (N = 14,994)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>≤19 (N = 143, n = 78, 54.5%)</td>
<td>41</td>
<td>52.6</td>
<td>37</td>
<td>47.4</td>
<td>16</td>
</tr>
<tr>
<td>20s (N = 6179, n = 3750, 60.7%)</td>
<td>2061</td>
<td>55.0</td>
<td>1689</td>
<td>45.0</td>
<td>939</td>
</tr>
<tr>
<td>30s (N = 5824, n = 3680, 66.8%)</td>
<td>2140</td>
<td>58.2</td>
<td>1540</td>
<td>41.8</td>
<td>965</td>
</tr>
<tr>
<td>40s (N = 1929, n = 1289, 66.8%)</td>
<td>782</td>
<td>60.7</td>
<td>507</td>
<td>39.3</td>
<td>311</td>
</tr>
<tr>
<td>50s (N = 713, n = 496, 69.6%)</td>
<td>319</td>
<td>64.3</td>
<td>177</td>
<td>35.7</td>
<td>112</td>
</tr>
<tr>
<td>60s (N = 174, n = 116, 66.7%)</td>
<td>78</td>
<td>67.2</td>
<td>38</td>
<td>32.8</td>
<td>24</td>
</tr>
<tr>
<td>≥70 (N = 32, n = 19, 59.4%)</td>
<td>6</td>
<td>31.6</td>
<td>13</td>
<td>68.4</td>
<td>4</td>
</tr>
<tr>
<td>Swab (N = 9073)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>≤19 (N = 89, n = 38, 42.7%)</td>
<td>22</td>
<td>57.9</td>
<td>16</td>
<td>42.1</td>
<td>6</td>
</tr>
<tr>
<td>20s (N = 3725, n = 2002, 53.7%)</td>
<td>1079</td>
<td>53.9</td>
<td>923</td>
<td>46.1</td>
<td>496</td>
</tr>
<tr>
<td>30s (N = 3547, n = 2012, 56.7%)</td>
<td>1156</td>
<td>57.5</td>
<td>856</td>
<td>42.5</td>
<td>530</td>
</tr>
<tr>
<td>40s (N = 1157, n = 698, 60.3%)</td>
<td>411</td>
<td>58.9</td>
<td>287</td>
<td>41.1</td>
<td>173</td>
</tr>
<tr>
<td>50s (N = 422, n = 264, 62.6%)</td>
<td>161</td>
<td>61.0</td>
<td>103</td>
<td>39.0</td>
<td>65</td>
</tr>
<tr>
<td>60s (N = 112, n = 68, 60.7%)</td>
<td>47</td>
<td>69.1</td>
<td>21</td>
<td>30.9</td>
<td>13</td>
</tr>
<tr>
<td>≥70 (N = 21, n = 12, 57.1%)</td>
<td>4</td>
<td>33.3</td>
<td>8</td>
<td>66.7</td>
<td>3</td>
</tr>
<tr>
<td>Tissue (N = 4050)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>≤19 (N = 37, n = 35, 94.6%)</td>
<td>15</td>
<td>42.9</td>
<td>20</td>
<td>57.1</td>
<td>10</td>
</tr>
<tr>
<td>20s (N = 1611, n = 1485, 92.2%)</td>
<td>830</td>
<td>55.9</td>
<td>655</td>
<td>44.1</td>
<td>380</td>
</tr>
<tr>
<td>30s (N = 1566, n = 1441, 92.0%)</td>
<td>850</td>
<td>59.0</td>
<td>591</td>
<td>41.0</td>
<td>384</td>
</tr>
<tr>
<td>40s (N = 562, n = 529, 94.1%)</td>
<td>329</td>
<td>62.2</td>
<td>200</td>
<td>37.8</td>
<td>126</td>
</tr>
<tr>
<td>50s (N = 221, n = 206, 93.2%)</td>
<td>139</td>
<td>67.5</td>
<td>67</td>
<td>32.5</td>
<td>42</td>
</tr>
<tr>
<td>60s (N = 44, n = 41, 93.2%)</td>
<td>28</td>
<td>68.3</td>
<td>13</td>
<td>31.7</td>
<td>8</td>
</tr>
<tr>
<td>≥70 (N = 9, n = 7, 77.8%)</td>
<td>2</td>
<td>28.6</td>
<td>5</td>
<td>71.4</td>
<td>1</td>
</tr>
<tr>
<td>Urine (N = 823)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>≤19 (N = 7, n = 2, 28.6%)</td>
<td>1</td>
<td>50.0</td>
<td>1</td>
<td>50.0</td>
<td>0</td>
</tr>
<tr>
<td>20s (N = 340, n = 67, 19.7%)</td>
<td>45</td>
<td>67.2</td>
<td>22</td>
<td>32.8</td>
<td>9</td>
</tr>
<tr>
<td>30s (N = 306, n = 56, 18.3%)</td>
<td>40</td>
<td>71.4</td>
<td>16</td>
<td>28.6</td>
<td>12</td>
</tr>
<tr>
<td>40s (N = 118, n = 19, 16.1%)</td>
<td>14</td>
<td>73.7</td>
<td>5</td>
<td>26.3</td>
<td>3</td>
</tr>
<tr>
<td>50s (N = 38, n = 9, 23.7%)</td>
<td>7</td>
<td>77.8</td>
<td>2</td>
<td>22.2</td>
<td>1</td>
</tr>
<tr>
<td>60s (N = 12, n = 3, 25.0%)</td>
<td>2</td>
<td>66.7</td>
<td>1</td>
<td>33.3</td>
<td>0</td>
</tr>
<tr>
<td>≥70 (N = 2, n = 0, 0%)</td>
<td>0</td>
<td>0.0</td>
<td>0</td>
<td>0.0</td>
<td>0</td>
</tr>
</tbody>
</table>

χ² = 81.502, p < 0.0001

χ² = 126.930, p < 0.0001

χ² = 49.5861, p < 0.0001

χ² = 73.5006, p < 0.0001

χ² = 27.7083, p = 0.0061

χ² = 66.1813, p < 0.0001

χ² = 3.8982, p = 0.9852

χ² = 25.5594, p = 0.3759

χ² = 14.2868, p = 0.1603

χ² = 25.1409, p = 0.1961

1 N, Total participants; n, Number of positive cases; %, Positivity rate.
2 Percentage refers to each case compared with the total number of positive cases.
3 The χ² value represents the difference between single and co-infection rates by age group in each specimen.
4 The χ² value represents the difference between single HPV infection and rates of co-infection with 2, 3 and ≥4 HPV genotypes by age group in each specimen.
3.6 Age-specific positivity rates of high-risk HPV infection according to genotype

Fig. 3 illustrates age-specific positivity rates of high-risk HPV infection according to genotype. The positivity rate for genotype 16 increased with age ($\chi^2 = 1012.028, p < 0.0001$). The positivity rates for all genotypes varied with age, decreasing in diversity with increasing age.

Further details on each specimen are presented in Supplementary Table 2.

4. Discussion

While considerable attention has been dedicated to HPV infection in women, studies focusing on the male population are lacking. To comprehensively understand this virus, a closer examination of the characteristics of infection in men is imperative [13, 14]. Therefore, this study used large-scale population-based data to determine the positivity rates, genotypes, and co-infection rates of HPV in Korean men.

The results of this study indicated that positivity rates consistently exceeded 50% across all age groups. The highest positivity rate was observed in individuals in their 50s, whereas the lowest rate was noted in teenagers. The reasons for the differences in HPV positivity rates among age groups may include differences in immunity depending on age and higher vaccination rates in young people.

An analysis of infection rates discriminated by sex in seven testing facilities in Iran comprising 2727 samples revealed a higher positivity rate in men than in women [15]. Conversely, a meta-analysis incorporating HPV data from 35 countries revealed an overall positivity rate of 31% (95% confidence interval: 27–35) for all HPV genotypes. The highest positivity rate was observed in young men in the age range of 25–29 years, and it stabilized or slightly decreased thereafter [16]. Previous studies have reported diverse positivity rates in different countries. One study in which the integrated positivity rates for each country varied widely (from 1% to 84%) suggests that regional differences, variations in sample types, and differences in testing methods contributed to these variations [17].

The high-risk genotype 16 accounted for a significant positivity rate of cases with increasing age. This supports previous findings suggesting that men may be a reservoir for HPV infection and a potential target for monitoring and that the risk of developing an HPV infection in women may persist across different age groups [18]. Therefore, HPV infection management should not be limited to younger sexually active age groups but should cover all ages.

In the present study, the number of genotypes infecting men varied with age. As age increased, the diversity of genotypes decreased, and the positivity rate for high-risk genotype 16 increased. As these genotypes are associated with cancer development, the role of men in female infections should not be overlooked, even with aging [19].

In this study, the most common HPV genotypes in men were 6 and 11, which are categorized as low-risk HPV genotypes. According to previous research on HPV genotypes in men in East and Southeast Asia, genotype 6 had the highest positivity rate, with genotype 11 being the sixth most common [16]. Additionally, Hoai et al. [20] reported positivity rates of 36.7% and 21.4% for genotypes 6 and 11, respectively, and identified them as the two most common low-risk genotypes. Although HPV genotypes 6 and 11 are classified as low risk, they are associated with genital warts and recurrent respiratory papillomatosis. Previous research has emphasized the importance of promoting the early use of HPV vaccines targeting genotypes 6 and 11 in the prevention of these conditions [21, 22].

The present study revealed a high positivity rate of HPV co-infections in men, with an overall positivity rate of 62.9%. The maximum number of co-infecting HPV genotypes was 10.

Although there is currently no clear explanation for the mechanism underlying co-infections, their occurrence has
been reported in previous studies. It is crucial not to overlook the causative roles of different HPV subtypes in various malignancies. Additionally, differences in variants between complex HPV genotypes due to co-infections with other HPV genotypes may be involved in this mechanism [23, 24].

4.1 Implications for clinical practice
In this study, men showed a high positivity rate of HPV infection across all age ranges. This represents a risk to their sexual partners in terms of increased risk of transmission and potential health implications. Therefore, efforts should be directed toward proactive prevention and control of infections, including those among non-heterosexual individuals. Additionally, there should be an increase in awareness, promotion of vaccination, and implementation of public education programs covering HPV, including those targeted at adolescents. By focusing efforts on all genders, these initiatives aim to reduce the disease burden and transmission risk, ultimately contributing to the prevention of cervical cancer [25, 26].

4.2 Study strengths
The strength of our study lies in the use of a large-scale participant-based dataset encompassing individuals from their teenage years to their 70s.

4.3 Limitations and scope for future studies
This study was constrained by limited data (restricted to sex, age and sample results) and lacked additional information on clinical symptoms or underlying conditions of the participants. Furthermore, samples used in this study included swabs and tissue and urine samples. The absence of a direct comparison between sample categories and adjustments for each sample type in comparison with other studies may impose limitations to the interpretation of the results and analyses. As the samples were mainly from patients who had visited the clinic due to a suspected STIs, it is not possible to assume that all the samples are representative of those from a population of healthy men.

5. Conclusions
Our analysis of HPV genotypes in a large dataset of Korean men revealed significant differences in positivity rates across various age groups. The most prevalent HPV genotypes were 6 and 11. Although genotypes 16 and 18 were associated with a lower average patient age, they accounted for a higher proportion of positive samples as patient age increased. The detected genotypes varied with age, with genotype 69 being the most frequently detected. Additionally, the occurrence of HPV co-infections was common. These findings underscore the importance of implementing HPV prevention and infection management strategies throughout the lifespan in men.

ABBREVIATIONS
HPV, human papillomavirus; IRB, Institutional Review Board.
AVAILABILITY OF DATA AND MATERIALS
The data utilized in this study were obtained from U2Bio laboratories. Due to company policy, we are unable to make the data publicly available. However, the data are accessible through the corresponding author upon reasonable request.

AUTHOR CONTRIBUTIONS
JH and HSS—made substantial contributions to the conception and design of the study, and these authors contributed equally to this study. JKK and JMK—made substantial contributions to the acquisition and analysis of the data. JKK—made a substantial contribution to the data analysis. JH, HSS and JMK—wrote the manuscript. All authors contributed to editorial changes in the manuscript. All authors read and approved the final manuscript.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE
This study was approved by the IRB of U2Bio (IRB No. 2023066) and conducted in accordance with the principles of the Declaration of Helsinki. As the data were analyzed retrospectively and personal information from the participants was not used, the requirement for obtaining informed consent was waived by the IRB of U2Bio.

ACKNOWLEDGMENT
We thank the employees at our testing center in U2Bio (Seoul, South Korea) for their assistance in accessing the HPV PCR assay data.

FUNDING
This research received no external funding.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

SUPPLEMENTARY MATERIAL
Supplementary material associated with this article can be found, in the online version, at Supplementary material associated with this article can be found, in the online version, at

REFERENCES


