Table 1Geographic coordinates (decimal degrees) of *Papio* sampling sites and sample sizes.

No. Taxon Country Site Code Sample size Longitude Latitude								
2 Ph Saudi Arabia Al Akhal Akl 6 39.859444 23.315556 3 Ph Saudi Arabia Baha 15 41.466667 20.016667 4 Ph Saudi Arabia Dhilafa Escp. Dhi 4 42.466667 17.933333 5 Ph Saudi Arabia Taif Tif 15 40.415833 21.270278 6 Ph Yemen Bura'a Forest A BuH 4 43.416667 14.866667 7 Ph Yemen Jebel Iraf Ira 1 44.250000 13.116667 9 Ph Yemen Jebel Raymah Ray 1 44.250000 13.16667 10 Ph Yemen Jebel Raymah Ray 1 44.250000 13.16667 10 Ph Yemen Jebel Raymah Ray 1 44.200000 13.583333 11 Ph Eritrea Abdur Aba 11 39.845850 15.12870 <tr< td=""><td>No.</td><td>Taxon</td><td>Country</td><td>Site</td><td>Code</td><td></td><td>Longitude</td><td>Latitude</td></tr<>	No.	Taxon	Country	Site	Code		Longitude	Latitude
3 Ph Saudi Arabia Baha 15 41.466667 20.016667 4 Ph Saudi Arabia Dhilafa Escp. Dhi 4 42.466667 17.93333 5 Ph Saudi Arabia Taif 15 40.415833 21.270278 6 Ph Yemen Bura'a Forest A BuH 4 43.416667 14.866667 7 Ph Yemen Bura'a Forest B BuL 5 43.866944 14.867222 8 Ph Yemen Jebel Raymah Ray 1 44.250000 13.116667 9 Ph Yemen Jebel Raymah Ray 1 44.200000 13.116667 10 Ph Yemen Jebel Raymah Ray 1 44.200000 13.116667 10 Ph Feritrea Abdur Abd 11 39.94845850 15.128570 13 Ph Eritrea Abdur Abd 11 39.9484580 15.758710 15<	1	Ph	Saudi Arabia	Abha	Abh	25	42.505228	18.216389
4 Ph Saudi Arabia Dhilafa Escp. Dhilafa Tif 4 42.466667 17.933333 5 Ph Saudi Arabia Taif Tif 15 40.415833 21.270278 6 Ph Yemen Bura'a Forest B Bull 43.416667 14.866667 7 Ph Yemen Jebel Iraf Ira 1 44.250000 13.116667 9 Ph Yemen Jebel Sabir Sab 1 44.200000 13.58333 10 Ph Yemen Jebel Sabir Sab 1 44.200000 13.583333 11 Ph Eritrea Mt. Abagamsei Aba 14 39.018620 15.349100 12 Ph Eritrea Abduur Abd 11 39.845850 15.128570 13 Ph Eritrea Ababet Afb 3 38.749583 16.120166 14 Ph Eritrea Ababet Afb 3 38.020380 15.57570	2	Ph	Saudi Arabia	Al Akhal	Akl	6	39.859444	23.315556
5 Ph Saudi Arabia Taif 15 40.415833 21.270278 6 Ph Yemen Bura'a Forest A BuH 4 43.416667 14.866667 7 Ph Yemen Jebel Iraf Ira 1 44.250000 13.116667 9 Ph Yemen Jebel Raymah Ray 1 43.433333 14.666667 10 Ph Yemen Jebel Sabir Sab 1 44.200000 13.583333 11 Ph Eritrea Mt. Abagamsei Aba 14 39.018620 15.349100 12 Ph Eritrea Abdur Abd 13 38.749583 16.120166 14 Ph Eritrea Abdur Afb 3 38.749583 16.120166 14 Ph Eritrea Abdur Afb 3 38.749583 16.120166 14 Ph Eritrea Raeat Bea 2 38.094270 15.671570 15<	3	Ph	Saudi Arabia	Baha	Bah	15	41.466667	20.016667
6 Ph Yemen Bura'a Forest A BuH 4 43.416667 14.866667 7 Ph Yemen Bura'a Forest B BuL 5 43.866944 14.867222 8 Ph Yemen Jebel Iraf Ira 1 44.250000 13.116667 9 Ph Yemen Jebel Sabir Sab 1 43.433333 14.666667 10 Ph Eritrea Mt. Abagamsei Aba 14 39.018620 15.349100 12 Ph Eritrea Abdur Abd 11 39.845850 15.128570 13 Ph Eritrea Afabet Afb 3 38.749583 16.120166 14 Ph Eritrea Afabet Afb 3 38.749583 16.120166 14 Ph Eritrea Afabet Afb 3 38.749583 16.120166 15 Ph Eritrea Dada (Bolo) Dad 13 43.2508889 13.129630	4	Ph	Saudi Arabia	Dhilafa Escp.	Dhi	4	42.466667	17.933333
7 Ph Yemen Bura'a Forest B Bul. 5 43.866944 14.867222 8 Ph Yemen Jebel Iraf Ira 1 44.250000 13.116667 9 Ph Yemen Jebel Sabir Sab 1 44.200000 13.583333 11 Ph Eritrea Mt. Abagamsei Aba 14 39.018620 15.349100 12 Ph Eritrea Abdur Abd 11 39.845850 15.128570 13 Ph Eritrea Afabet Afb 3 38.749583 16.120166 14 Ph Eritrea Barka Bridge Bbr 7 38.020380 15.555120 15 Ph Eritrea Dada (Bolo) Dad 13 42.508889 13.129630 17 Ph Eritrea Debresina Deb 3 38.825930 15.705350 18 Ph Eritrea Deptesina Deg 3 38.9454580 15.373700 <td>5</td> <td>Ph</td> <td>Saudi Arabia</td> <td>Taif</td> <td>Tif</td> <td>15</td> <td>40.415833</td> <td>21.270278</td>	5	Ph	Saudi Arabia	Taif	Tif	15	40.415833	21.270278
8 Ph Yemen Jebel Iraf Ira 1 44.250000 13.116667 9 Ph Yemen Jebel Raymah Ray 1 43.433333 14.666667 10 Ph Yemen Jebel Sabir Sab 1 44.200000 13.583333 11 Ph Eritrea Mt. Abagamsei Aba 14 39.018620 15.349100 12 Ph Eritrea Abdur Abd 11 39.845850 15.128570 13 Ph Eritrea Afabet Afb 3 38.749583 16.120166 14 Ph Eritrea Barka Bridge Bbr 7 38.020380 15.555120 15 Ph Eritrea Dadd (Bolo) Dad 13 42.508889 13.129630 17 Ph Eritrea Debresina Deb 3 38.825930 15.5759080 18 Ph Eritrea Durfo Dur 7 38.964580 15.379080	6	Ph	Yemen	Bura'a Forest A	BuH	4	43.416667	14.866667
9 Ph Yemen Jebel Raymah Ray 1 43.433333 14.666667 10 Ph Yemen Jebel Sabir Sab 1 44.200000 13.583333 11 Ph Eritrea Mt. Abagamsei Aba 14 39.018620 15.349100 12 Ph Eritrea Abdur Abd 11 39.845850 15.128570 13 Ph Eritrea Afabet Afb 3 38.749583 16.120166 14 Ph Eritrea Barka Bridge Bbr 7 38.020380 15.555120 15 Ph Eritrea Dada (Bolo) Dad 13 42.508889 13.129630 17 Ph Eritrea Debresina Deb 3 38.25930 15.579508 18 Ph Eritrea Durfo Dur 7 38.964580 15.279508 19 Ph Eritrea Durfo Dur 7 38.964580 15.579080 <td>7</td> <td>Ph</td> <td>Yemen</td> <td>Bura'a Forest B</td> <td>BuL</td> <td>5</td> <td>43.866944</td> <td>14.867222</td>	7	Ph	Yemen	Bura'a Forest B	BuL	5	43.866944	14.867222
10	8	Ph	Yemen	Jebel Iraf	Ira	1	44.250000	13.116667
11 Ph Eritrea Mt. Abagamsei Aba 14 39.018620 15.349100 12 Ph Eritrea Abdur Abd 11 39.845850 15.128570 13 Ph Eritrea Afabet Afb 3 38.749583 16.120166 14 Ph Eritrea Barka Bridge Bbr 7 38.020380 15.555120 15 Ph Eritrea Dada (Bolo) Dad 13 42.508889 13.129630 16 Ph Eritrea Debresina Deb 3 38.825930 15.705350 18 Ph Eritrea Dogali Dog 6 39.284730 15.579080 19 Ph Eritrea Durfo Dur 7 38.964580 15.373700 20 Ph Eritrea Durfo Dur 7 38.944450 15.614420 21 Ph Eritrea Fill Bridge Fil 6 38.944450 15.614420 <td>9</td> <td>Ph</td> <td>Yemen</td> <td>Jebel Raymah</td> <td>Ray</td> <td>1</td> <td>43.433333</td> <td>14.666667</td>	9	Ph	Yemen	Jebel Raymah	Ray	1	43.433333	14.666667
12 Ph Eritrea Abdur Abd 11 39.845850 15.128570 13 Ph Eritrea Afabet Afb 3 38.749583 16.120166 14 Ph Eritrea Barka Bridge Bbr 7 38.020380 15.555120 15 Ph Eritrea Baeat Bea 2 38.020380 15.5755120 16 Ph Eritrea Dada (Bolo) Dad 13 42.508889 13.129630 17 Ph Eritrea Debresina Deb 3 38.825930 15.705350 18 Ph Eritrea Dogali Dog 6 39.284730 15.575300 18 Ph Eritrea Durfo Dur 7 38.964580 15.373700 19 Ph Eritrea Fulfo Dur 7 38.964580 15.373700 20 Ph Eritrea Furrus Fur 9 38.971150 15.611420	10	Ph	Yemen	Jebel Sabir		1	44.200000	13.583333
13 Ph Eritrea Afabet Afb 3 38.749583 16.120166 14 Ph Eritrea Barka Bridge Bbr 7 38.020380 15.555120 15 Ph Eritrea R. Baeat Bea 2 38.020370 15.671570 16 Ph Eritrea Dada (Bolo) Dad 13 42.508889 13.129630 17 Ph Eritrea Debresina Deb 3 38.825930 15.705350 18 Ph Eritrea Dogali Dog 6 39.284730 15.579080 19 Ph Eritrea Durfo Dur 7 38.964580 15.373700 20 Ph Eritrea Furrus Fur 9 38.944450 15.614420 21 Ph Eritrea Furrus Fur 9 38.824070 15.821430 22 Ph Eritrea Halhal Hal 7 38.314330 15.941370	11	Ph	Eritrea	Mt. Abagamsei	Aba	14	39.018620	15.349100
14 Ph Eritrea Barka Bridge Bbr 7 38.020380 15.555120 15 Ph Eritrea R. Baeat Bea 2 38.094270 15.671570 16 Ph Eritrea Dada (Bolo) Dad 13 42.508889 13.129630 17 Ph Eritrea Debresina Deb 3 38.825930 15.579080 18 Ph Eritrea Dogali Dog 6 39.284730 15.579080 19 Ph Eritrea Durfo Dur 7 38.964580 15.373700 20 Ph Eritrea Filfil Bridge Fil 6 38.944450 15.614420 21 Ph Eritrea Geleb Gel 7 38.314330 15.911480 22 Ph Eritrea Geleb Gel 7 38.344450 15.614420 23 Ph Eritrea Ag Himbol Hal 7 38.314330 15.941570	12	Ph	Eritrea	Abdur	Abd	11	39.845850	15.128570
15 Ph Eritrea R. Baeat Bea 2 38.094270 15.671570 16 Ph Eritrea Dada (Bolo) Dad 13 42.508889 13.129630 17 Ph Eritrea Debresina Deb 3 38.825930 15.705350 18 Ph Eritrea Dogali Dog 6 39.284730 15.579080 19 Ph Eritrea Durfo Dur 7 38.964580 15.373700 20 Ph Eritrea Filfill Bridge Fil 6 38.944450 15.614420 21 Ph Eritrea Geleb Gel 7 38.824070 15.821430 22 Ph Eritrea Geleb Gel 7 38.824070 15.821430 23 Ph Eritrea Halhal Hal 7 38.351230 15.941370 24 Ph Eritrea Af Himbol Him 9 37.397100 15.945050 <	13	Ph	Eritrea	Afabet	Afb	3	38.749583	16.120166
16 Ph Eritrea Dada (Bolo) Dad 13 42.508889 13.129630 17 Ph Eritrea Debresina Deb 3 38.825930 15.705350 18 Ph Eritrea Dogali Dog 6 39.284730 15.579080 19 Ph Eritrea Durfo Dur 7 38.964580 15.373700 20 Ph Eritrea Filfil Bridge Fil 6 38.944450 15.614420 21 Ph Eritrea Geleb Gel 7 38.824070 15.821430 22 Ph Eritrea Geleb Gel 7 38.824070 15.941370 23 Ph Eritrea Halhal Hal 7 38.314330 15.941370 24 Ph Eritrea Kubkub Kub 11 38.632170 15.945980 25 Ph Eritrea Mensura Men 5 38.351230 15.445980	14	Ph	Eritrea	Barka Bridge	Bbr	7	38.020380	15.555120
17 Ph Eritrea Debresina Deb 3 38.825930 15.705350 18 Ph Eritrea Dogali Dog 6 39.284730 15.579080 19 Ph Eritrea Durfo Dur 7 38.964580 15.373700 20 Ph Eritrea Filffl Bridge Fil 6 38.944450 15.614420 21 Ph Eritrea Furrus Fur 9 38.971150 15.011480 22 Ph Eritrea Geleb Gel 7 38.824070 15.821430 23 Ph Eritrea Halhal Hal 7 38.314330 15.941370 24 Ph Eritrea Af Himbol Him 9 37.397100 15.945050 25 Ph Eritrea Kubkub Kub 11 38.632170 16.344820 26 Ph Eritrea Molki Mol 7 38.221700 14.990908	15	Ph	Eritrea	R. Baeat	Bea	2	38.094270	15.671570
18 Ph Eritrea Dogali Dog 6 39.284730 15.579080 19 Ph Eritrea Durfo Dur 7 38.964580 15.373700 20 Ph Eritrea Filfil Bridge Fil 6 38.944450 15.614420 21 Ph Eritrea Furrus Fur 9 38.971150 15.614420 22 Ph Eritrea Geleb Gel 7 38.824070 15.821430 23 Ph Eritrea Halhal Hal 7 38.314330 15.941370 24 Ph Eritrea Af Himbol Him 9 37.397100 15.945050 25 Ph Eritrea Kubkub Kub 11 38.632170 16.344820 26 Ph Eritrea Mensura Men 5 38.351230 15.445980 27 Ph Eritrea Molki Mol 7 38.221700 14.909080	16	Ph	Eritrea	Dada (Bolo)	Dad	13	42.508889	13.129630
19 Ph Eritrea Durfo Dur 7 38.964580 15.373700 20 Ph Eritrea Filfil Bridge Fil 6 38.944450 15.614420 21 Ph Eritrea Furrus Fur 9 38.971150 15.011480 22 Ph Eritrea Geleb Gel 7 38.824070 15.821437 23 Ph Eritrea Halhal Hal 7 38.314330 15.941370 24 Ph Eritrea Af Himbol Him 9 37.397100 15.945050 25 Ph Eritrea Kubkub Kub 11 38.632170 16.344820 26 Ph Eritrea Mensura Men 5 38.351230 15.445980 27 Ph Eritrea Molki Mol 7 38.221700 14.9909080 28 PX Eritrea R. Shackat Sha 4 37.499350 14.983100	17	Ph	Eritrea	Debresina	Deb	3	38.825930	15.705350
20 Ph Eritrea Filfil Bridge Fil 6 38.944450 15.614420 21 Ph Eritrea Furrus Fur 9 38.971150 15.011480 22 Ph Eritrea Geleb Gel 7 38.824070 15.821430 23 Ph Eritrea Halhal Hal 7 38.314330 15.941370 24 Ph Eritrea Af Himbol Him 9 37.397100 15.945050 25 Ph Eritrea Kubkub Kub 11 38.632170 16.344820 26 Ph Eritrea Mensura Men 5 38.351230 15.445980 27 Ph Eritrea Molki Mol 7 38.221700 14.998080 28 PX Eritrea R. Shackat Sha 4 37.499350 14.983100 29 Pa Eritrea R. Shackat Sha 4 37.499350 14.983100 <t< td=""><td>18</td><td>Ph</td><td>Eritrea</td><td>Dogali</td><td>Dog</td><td>6</td><td>39.284730</td><td>15.579080</td></t<>	18	Ph	Eritrea	Dogali	Dog	6	39.284730	15.579080
21 Ph Eritrea Furrus Fur 9 38.971150 15.011480 22 Ph Eritrea Geleb Gel 7 38.824070 15.821430 23 Ph Eritrea Halhal Halhal 7 38.314330 15.941370 24 Ph Eritrea Af Himbol Him 9 37.397100 15.945050 25 Ph Eritrea Kubkub Kub 11 38.632170 16.344820 26 Ph Eritrea Mensura Men 5 38.351230 15.445980 27 Ph Eritrea Molki Mol 7 38.22170 14.999080 28 PX Eritrea R. Shackat Sha 4 37.499350 14.983100 29 Pa Eritrea R. Griset Gri 8 36.760180 14.883220 30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 <tr< td=""><td>19</td><td>Ph</td><td>Eritrea</td><td>Durfo</td><td>Dur</td><td>7</td><td>38.964580</td><td>15.373700</td></tr<>	19	Ph	Eritrea	Durfo	Dur	7	38.964580	15.373700
22 Ph Eritrea Geleb Gel 7 38.824070 15.821430 23 Ph Eritrea Halhal Hal 7 38.314330 15.941370 24 Ph Eritrea Kubkub Kub 11 38.31230 15.945050 25 Ph Eritrea Kubkub Kub 11 38.632170 16.344820 26 Ph Eritrea Mensura Men 5 38.351230 15.445980 27 Ph Eritrea Molki Mol 7 38.221700 14.909080 28 PX Eritrea R. Shackat Sha 4 37.499350 14.9983100 29 Pa Eritrea R. Griset Gri 8 36.760180 14.883220 30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 31 Pa Eritrea Haykota Hay 17 37.066000 15.145100	20	Ph	Eritrea	Filfil Bridge	Fil	6	38.944450	15.614420
23 Ph Eritrea Halhal Hal 7 38.314330 15.941370 24 Ph Eritrea Af Himbol Him 9 37.397100 15.945050 25 Ph Eritrea Kubkub Kub 11 38.632170 16.344820 26 Ph Eritrea Mensura Men 5 38.351230 15.445980 27 Ph Eritrea Molki Mol 7 38.221700 14.909080 28 PX Eritrea R. Shackat Sha 4 37.499350 14.983100 29 Pa Eritrea R. Griset Gri 8 36.760180 14.883220 30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 31 Pa Eritrea Haykota Hay 17 37.066000 15.156950 32 Pa Eritrea Tesseney Tes 9 36.701420 15.145100	21	Ph	Eritrea	Furrus	Fur	9	38.971150	15.011480
24 Ph Eritrea Af Himbol Him 9 37.397100 15.945050 25 Ph Eritrea Kubkub Kub 11 38.632170 16.344820 26 Ph Eritrea Mensura Men 5 38.351230 15.445980 27 Ph Eritrea Molki Mol 7 38.221700 14.909080 28 PX Eritrea R. Shackat Sha 4 37.499350 14.983100 29 Pa Eritrea R. Griset Gri 8 36.760180 14.983220 30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 31 Pa Eritrea Haykota Hay 17 37.066000 15.156950 32 Pa Eritrea Tesseney Tes 9 36.701420 15.145100 33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 <td>22</td> <td>Ph</td> <td>Eritrea</td> <td>Geleb</td> <td>Gel</td> <td>7</td> <td>38.824070</td> <td>15.821430</td>	22	Ph	Eritrea	Geleb	Gel	7	38.824070	15.821430
25 Ph Eritrea Kubkub Kub 11 38.632170 16.344820 26 Ph Eritrea Mensura Men 5 38.351230 15.445980 27 Ph Eritrea Molki Mol 7 38.221700 14.909080 28 PX Eritrea R. Shackat Sha 4 37.499350 14.908100 29 Pa Eritrea R. Griset Gri 8 36.760180 14.883220 30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 31 Pa Eritrea Haykota Hay 17 37.066000 15.156950 32 Pa Eritrea Tesseney Tes 9 36.701420 15.145100 33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 34 Ph Ethiopia Mieso Mie 7 40.764083 9.203533	23	Ph	Eritrea	Halhal	Hal	7	38.314330	15.941370
26 Ph Eritrea Mensura Men 5 38.351230 15.445980 27 Ph Eritrea Molki Mol 7 38.221700 14.909080 28 PX Eritrea R. Shackat Sha 4 37.499350 14.983100 29 Pa Eritrea R. Griset Gri 8 36.760180 14.883220 30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 31 Pa Eritrea Haykota Hay 17 37.066000 15.156950 32 Pa Eritrea Tesseney Tes 9 36.701420 15.145100 33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 34 Ph Ethiopia Mieso Mie 7 40.764083 9.203533 36 PX Ethiopia Mwash Falls AFa 5 40.019167 8.842683 <td>24</td> <td>Ph</td> <td>Eritrea</td> <td>Af Himbol</td> <td>Him</td> <td>9</td> <td>37.397100</td> <td>15.945050</td>	24	Ph	Eritrea	Af Himbol	Him	9	37.397100	15.945050
27 Ph Eritrea Molki Mol 7 38.221700 14.909080 28 PX Eritrea R. Shackat Sha 4 37.499350 14.983100 29 Pa Eritrea R. Griset Gri 8 36.760180 14.883220 30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 31 Pa Eritrea Haykota Hay 17 37.066000 15.156950 32 Pa Eritrea Tesseney Tes 9 36.701420 15.156950 33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 34 Ph Ethiopia Mieso Mie 7 40.764083 9.20533 36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Adami Tulu Ada 4 38.714933 7.825583 <	25	Ph	Eritrea	Kubkub	Kub	11	38.632170	16.344820
28 PX Eritrea R. Shackat Sha 4 37.499350 14.983100 29 Pa Eritrea R. Griset Gri 8 36.760180 14.883220 30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 31 Pa Eritrea Haykota Hay 17 37.066000 15.1565100 32 Pa Eritrea Tesseney Tes 9 36.701420 15.145100 33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 34 Ph Ethiopia Gerba Luku Ger 10 41.534000 9.587400 35 Ph Ethiopia Mieso Mie 7 40.764083 9.203533 36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Adami Tulu Ada 4 38.714933 7.825583 <td>26</td> <td>Ph</td> <td>Eritrea</td> <td>Mensura</td> <td>Men</td> <td>5</td> <td>38.351230</td> <td>15.445980</td>	26	Ph	Eritrea	Mensura	Men	5	38.351230	15.445980
29 Pa Eritrea R. Griset Gri 8 36.760180 14.883220 30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 31 Pa Eritrea Haykota Hay 17 37.066000 15.156950 32 Pa Eritrea Tesseney Tes 9 36.701420 15.145100 33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 34 Ph Ethiopia Gerba Luku Ger 10 41.534000 9.587400 35 Ph Ethiopia Mieso Mie 7 40.764083 9.203533 36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Wolenkiti Wol 5 39.487883 8.694583 38 Pa Ethiopia Alambada Ala 3 38.747683 7.504633	27	Ph	Eritrea	Molki	Mol	7	38.221700	14.909080
30 Pa Eritrea R. Hadejemi Had 6 36.907100 14.358270 31 Pa Eritrea Haykota Hay 17 37.066000 15.156950 32 Pa Eritrea Tesseney Tes 9 36.701420 15.145100 33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 34 Ph Ethiopia Gerba Luku Ger 10 41.534000 9.587400 35 Ph Ethiopia Mieso Mie 7 40.764083 9.203533 36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Wolenkiti Wol 5 39.487883 8.694583 38 Pa Ethiopia Adambada Ala 3 38.747683 7.504633 40 Pa Ethiopia Managasha 1 Mng 1 38.531250 8.968383	28	PX	Eritrea	R. Shackat	Sha	4	37.499350	14.983100
31 Pa Eritrea Haykota Hay 17 37.066000 15.156950 32 Pa Eritrea Tesseney Tes 9 36.701420 15.145100 33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 34 Ph Ethiopia Gerb Luku Ger 10 41.534000 9.587400 35 Ph Ethiopia Mieso Mie 7 40.764083 9.203533 36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Wolenkiti Wol 5 39.487883 8.694583 38 Pa Ethiopia Adami Tulu Ada 4 38.714933 7.825583 39 Pa Ethiopia Alambada Ala 3 38.747683 7.504633 40 Pa Ethiopia Managasha 1 Mng 1 38.531250 8.968383	29	Pa	Eritrea	R. Griset	Gri	8	36.760180	14.883220
32 Pa Eritrea Tesseney Tes 9 36.701420 15.145100 33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 34 Ph Ethiopia Gerba Luku Ger 10 41.534000 9.587400 35 Ph Ethiopia Mieso Mie 7 40.764083 9.203533 36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Wolenkiti Wol 5 39.487883 8.694583 38 Pa Ethiopia Adami Tulu Ada 4 38.714933 7.825583 39 Pa Ethiopia Alambada Ala 3 38.747683 7.504633 40 Pa Ethiopia Managasha 1 Mig 1 38.583333 9.083333 41 Pa Ethiopia Managasha 2 Man 6 38.571250 8.968383 <td>30</td> <td>Pa</td> <td>Eritrea</td> <td>R. Hadejemi</td> <td>Had</td> <td>6</td> <td>36.907100</td> <td>14.358270</td>	30	Pa	Eritrea	R. Hadejemi	Had	6	36.907100	14.358270
33 Ph Ethiopia Awash Station ASt 5 40.177750 8.992683 34 Ph Ethiopia Gerba Luku Ger 10 41.534000 9.587400 35 Ph Ethiopia Mieso Mie 7 40.764083 9.203533 36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Wolenkiti Wol 5 39.487883 8.694583 38 Pa Ethiopia Adami Tulu Ada 4 38.714933 7.825583 39 Pa Ethiopia Alambada Ala 3 38.747683 7.504633 40 Pa Ethiopia Managasha 1 Mig 1 38.583333 9.083333 41 Pa Ethiopia Managasha 2 Man 6 38.571250 8.968383 42 Pa Ethiopia Wendo Genet Wen 1 38.649650 7.071267	31	Pa	Eritrea	Haykota	Hay	17	37.066000	15.156950
34 Ph Ethiopia Gerba Luku Ger 10 41.534000 9.587400 35 Ph Ethiopia Mieso Mie 7 40.764083 9.203533 36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Wolenkiti Wol 5 39.487883 8.694583 38 Pa Ethiopia Adami Tulu Ada 4 38.714933 7.825583 39 Pa Ethiopia Alambada Ala 3 38.747683 7.504633 40 Pa Ethiopia Managasha 1 Mmg 1 38.583333 9.083333 41 Pa Ethiopia Managasha 2 Man 6 38.571250 8.968383 42 Pa Ethiopia Wendo Genet Wen 1 38.649650 7.071267	32	Pa	Eritrea	Tesseney	Tes	9	36.701420	15.145100
35 Ph Ethiopia Mieso Mie 7 40.764083 9.203533 36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Wolenkiti Wol 5 39.487883 8.694583 38 Pa Ethiopia Adami Tulu Ada 4 38.714933 7.825583 39 Pa Ethiopia Alambada Ala 3 38.747683 7.504633 40 Pa Ethiopia Managasha 1 Mng 1 38.583333 9.083333 41 Pa Ethiopia Managasha 2 Man 6 38.571250 8.968383 42 Pa Ethiopia Wendo Genet Wen 1 38.649650 7.071267	33	Ph	Ethiopia	Awash Station	ASt	5	40.177750	8.992683
36 PX Ethiopia Awash Falls AFa 5 40.019167 8.842683 37 PX Ethiopia Wolenkiti Wol 5 39.487883 8.694583 38 Pa Ethiopia Adami Tulu Ada 4 38.714933 7.825583 39 Pa Ethiopia Alambada Ala 3 38.747683 7.504633 40 Pa Ethiopia Managasha 1 Mng 1 38.583333 9.083333 41 Pa Ethiopia Managasha 2 Man 6 38.571250 8.968383 42 Pa Ethiopia Wendo Genet Wen 1 38.649650 7.071267	34	Ph	Ethiopia	Gerba Luku	Ger	10	41.534000	9.587400
37 PX Ethiopia Wolenkiti Wol 5 39.487883 8.694583 38 Pa Ethiopia Adami Tulu Ada 4 38.714933 7.825583 39 Pa Ethiopia Alambada Ala 3 38.747683 7.504633 40 Pa Ethiopia Managasha 1 Mng 1 38.583333 9.083333 41 Pa Ethiopia Managasha 2 Man 6 38.571250 8.968383 42 Pa Ethiopia Wendo Genet Wen 1 38.649650 7.071267	35	Ph	Ethiopia	Mieso	Mie	7	40.764083	9.203533
38 Pa Ethiopia Adami Tulu Ada 4 38.714933 7.825583 39 Pa Ethiopia Alambada Ala 3 38.747683 7.504633 40 Pa Ethiopia Managasha 1 Mng 1 38.583333 9.083333 41 Pa Ethiopia Managasha 2 Man 6 38.571250 8.968383 42 Pa Ethiopia Wendo Genet Wen 1 38.649650 7.071267	36	PX	Ethiopia	Awash Falls	AFa	5	40.019167	8.842683
39 Pa Ethiopia Alambada Ala 3 38,747683 7.504633 40 Pa Ethiopia Managasha 1 Mng 1 38,583333 9.083333 41 Pa Ethiopia Managasha 2 Man 6 38,571250 8,968383 42 Pa Ethiopia Wendo Genet Wen 1 38,649650 7,071267	37	PX	Ethiopia	Wolenkiti	Wol	5	39.487883	8.694583
40 Pa Ethiopia Managasha 1 Mng 1 38.583333 9.083333 41 Pa Ethiopia Managasha 2 Man 6 38.571250 8.968383 42 Pa Ethiopia Wendo Genet Wen 1 38.649650 7.071267	38	Pa	Ethiopia	Adami Tulu	Ada	4	38.714933	7.825583
41 Pa Ethiopia Managasha 2 Man 6 38.571250 8.968383 42 Pa Ethiopia Wendo Genet Wen 1 38.649650 7.071267	39	Pa	Ethiopia	Alambada	Ala	3	38.747683	7.504633
42 Pa Ethiopia Wendo Genet Wen 1 38.649650 7.071267	40	Pa	Ethiopia	Managasha 1	Mng	1	38.583333	9.083333
		Pa	Ethiopia	Managasha 2			38.571250	8.968383
43 Pc Somalia Webi Shebelli Web 1 45.433333 2.420833	42	Pa	Ethiopia	Wendo Genet		1	38.649650	7.071267
	43	Pc	Somalia	Webi Shebelli	Web	1	45.433333	2.420833

Ph = Papio hamadryas; Pa = P. anubis; PX = phenotypic hybrids between P. hamadryas and P. anubis; Pc = P. cynocephalus. Longitude and latitude in decimal degrees.

To investigate whether the Arabian baboon population expanded after the colonization event, we calculated mismatch distributions for both Arabian clades in Arlequin 3.5.1.3 (Excoffier and Lischer, 2010) with 1000 bootstraps. We tested both the model for demographic expansion and the model for spatial expansion. We then calculated the time since expansion with $\tau=2\mu t$ (μ : mutation rate, t: number of generations since expansion). Here we applied a generation time of 12 years (Rogers and Kidd, 1996) and the specific mutation rate of primate HVRI of 15–20% per million years (Jensen-Seaman and Kidd, 2001).

To estimate divergence times between clades, we concatenated the Brown Region, cyt b, and HVRI sequences (n=70), and applied a Bayesian Markov Chain Monte Carlo method, which employs a relaxed molecular clock approach (Drummond et al., 2006) as implemented in BEAST 1.6.1 (Drummond and Rambaut, 2007). The three loci were partitioned, each with its optimal nucleotide substitution model (Brown Region: TrN+G; cyt b: HKY+G; HVRI: HKY+I+G) as chosen with the Bayesian information criterion (BIC) in jModeltest 0.1.1 (Posada, 2008). We assumed a relaxed uncorrelated lognormal model of lineage variation and a Birth-Death Process prior for branching rates. As a calibration point,

we applied the fossil-based split of *Theropithecus* and *Papio* 5.0 ± 1.0 mya (Jablonski et al., 2008; Frost et al., 2014). Four replicates were run for 25 million generations with tree and parameter sampling occurring every 100 generations. The adequacy of a 10% burn-in and convergence of all parameters was assessed by visual inspection of the trace of the parameters across generations using TRACER 1.5 (Rambaut et al., 2003). The sampling distributions were combined (25% burn-in) using LogCombiner 1.6.1 (Rambaut and Drummond, 2002a). A consensus chronogram with node height distribution was generated and visualized with TreeAnnotator 1.6.1 (Rambaut and Drummond, 2002b) and FigTree 1.3.1 (Rambaut, 2006).

Results

The 294 baboon samples comprised 109 HVRI haplotypes. The subset of 73 samples for which we analysed the Brown Region, cyt *b*, and HVRI, comprised 52 haplotypes.

Haplotype network

The HVRI haplotype network reveals three major clades (Fig. 3). Clade X is strictly African and consists of Eritrean and a few Ethiopian hamadryas baboons, and phenotypical *P. hamadryas* × *P. anubis* hybrids from Ethiopia. Clade Y is more complex, encompassing Eritrean hamadryas and olive baboons, Eritrean hybrids, and Arabian hamadryas baboons. Clade Z comprises Ethiopian, Eritrean, and Arabian hamadryas baboons. Two Arabian clades are identifiable. Clade Arab_Y comprises four haplotypes and clusters closely with Eritrean baboons. Clade Arab_Z consists mainly of haplotypes found in Arabia but also some haplotypes found in Eritrea from sampling locations closest to the Bab-el-Mandab Strait (Dad) and one haplotype from Gerba Luku, Ethiopia (0317PHGer). Clade Arab_Z clusters more closely with Ethiopian baboons.

Population genetics of Arabian baboons

Whereas the three northern Arabia sampling locations (Akla, Taif, and Baha) harbour only haplotypes of Clade Arab_Z, both Clades Arab_Z and Arab_Y are represented in all other locations in Arabia (Fig. 4). One haplotype (H1) of Clade Arab_Z is found in every sampling location in Arabia.

Haplotype diversity and nucleotide diversity are both significantly higher in the African than in the Arabian hamadryas baboon populations ($n_{\rm Africa}=149,\ n_{\rm Arabia}=77,\ {\rm Hd}_{\rm Africa}\pm{\rm SD}=0.983\pm0.003,\ {\rm Hd}_{\rm Arabia}\pm{\rm SD}=0.871\pm0.026,\ p<0.001;\ \pi_{\rm Africa}\pm{\rm SD}=0.04251\pm0.00088,\ \pi_{\rm Arabia}\pm{\rm SD}=0.01920\pm0.00243,\ p<0.001).$ Haplotype diversity and nucleotide diversity are both significantly higher (p<0.001) in Clade Arab_Z (n=61) than in Clade Arab_Y (n=16): (${\rm Hd}_{\rm Z}\pm{\rm SD}=0.825\pm0.040,\ {\rm Hd}_{\rm Y}\pm{\rm SD}=0.533\pm0.142)$ and $\pi_{\rm Z}\pm{\rm SD}=0.00431\pm{\rm S0.00046},\ \pi_{\rm Y}\pm{\rm SD}=0.00218\pm0.00076.$

When genetic diversity for Arabian hamadryas baboons is depicted from south to north, a decrease is observed in nucleotide diversity but not in haplotype diversity (Fig. 5). Both Arabian clades probably underwent a population expansion, as neither the demographic nor the spatial expansion model is rejected at $\alpha=5\%$ (Table 2). The expansion of Clade Arab_Z occurred twice as early as the expansion of Clade Arab_Y, as indicated by a τ value, which is twice as high (Table 2).

Phylogenetic tree and divergence time estimates

Similar to the network, the phylogenetic tree reconstruction, based on concatenated Brown + cyt b + HVRI sequences, reveals the three distinct Clades X, Y, and Z, all of which include African