Figures and figure supplements

Evolution of gene dosage on the Z-chromosome of schistosome parasites

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Figure 1. Shared and lineage-specific evolutionary strata on the Z-chromosome. The phylogeny of the three species is represented on the left. The female:male (F:M) ratio of coverage (y-axis) along the Z-chromosome of S. mansoni (x-axis) is shown for S. japonicum scaffolds (A) and S. mansoni 10 kb windows (B). Female coverage is shown for S. haematobium scaffolds (C). All species share an ancestral Z-linked stratum S0 (marked in orange). The stratum S1jap (in green) is specific to the Asian lineage represented by S. japonicum. The stratum S1mans (in blue) is specific to the African lineage, represented by S. mansoni and S. haematobium. Dot color is attributed depending on the window/scaffold location within each species: Z-specific regions in orange, pseudoautosomal regions in grey, and ambiguous regions in beige.

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Figure 2. Patterns of expression on the Z and autosomes of *S. japonicum* and *S. mansoni*. Z-linked and autosomal gene expression patterns are shown for *S. japonicum* (A-D) and *S. mansoni* (E-H), in undifferentiated schistosomula and sexually mature adults. In panels A, C, E, and G, Fem-Z and Male-Z refer to the expression of Z-linked genes in females and males, respectively, and Fem-A and Male-A to the expression of the autosomal genes in females and males. In panels B, D, F, and H, Z refers to Z-linked genes and A to autosomal genes. In all conditions, a strong male bias is observed for the Z-linked genes (B, D, F, H). This male-biased expression of the Z-linked genes is accompanied by both an under-expression in females and an over-expression in males, compared to the level of autosomal expression (A, C, E, G). The level of significance of each comparison (Wilcoxon rank sum test with continuity correction) is indicated by asterisks: *p-value<0.05, **p-value<0.001, ***p-value<0.0001.

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Figure 2—figure supplement 1. Adult expression patterns (RPKM>1, exhaustive strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) *S. mansoni* females, (B) *S. mansoni* males, (C) *S. mansoni* female:male, (D) *S. japonicum* females, (E) *S. japonicum* males, (F) *S. japonicum* female:male, (G) Female expression in *S. japonicum* divided by female expression in *S. mansoni*, (H) Male expression in *S. japonicum* divided by male expression in *S. mansoni*, (I) female:male ratio of expression in *S. japonicum* divided by female:male ratio of expression in *S. mansoni*. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p*-value<0.05, **p*-value<0.001, ***p*-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns, only genes with RPKM >1 were used.

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ADULTS - RPKM>0 - Strata Method2 (Exhaustive)

A) Females - S. mansoni

B) Males - S. mansoni

C) F:M ratio - S. mansoni

D) Females - S. japonicum

E) Males - S. japonicum

F) F:M ratio - S. japonicum

G) Females - S.jap:S.mans

H) Males - S.jap:S.mans

I) F:M ratio - S.jap:S.mans

Figure 2—figure supplement 2. Adult expression patterns (RPKM>0, exhaustive strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female: male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female: male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female: male ratio of expression in S. japonicum divided by female: male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns; only genes with RPKM >0 were used.

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Figure 2—figure supplement 3. Adult expression patterns (RPKM>1, stringent strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female:male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female: male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female:male ratio of expression in S. japonicum divided by female:male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes previously mapped to the ZW linkage group were assigned to each Z-chromosome stratum based on their coverage patterns (stringent classification); only genes with RPKM >1 were used.

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Figure 2—figure supplement 4. Adult expression patterns (RPKM>0, stringent strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female: male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female: male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female:male ratio of expression in S. japonicum divided by female:male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes previously mapped to the ZW linkage group were assigned to each Z-chromosome stratum based on their coverage patterns (stringent classification); only genes with RPKM >0 were used.

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Figure 2—figure supplement 5. Adult expression patterns (RPKM>1, exhaustive strata, Wormbase orthologs) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female:male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female:male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female:male ratio of expression in S. japonicum divided by female:male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns; only genes with RPKM >0 were used. This figure differs from Figure 2-figure supplement 1 as the Wormbase Parasite list 1:1 orthologs was used instead of our own reciprocal best hit results.

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Figure 2—figure supplement 6. Adult expression patterns (TPM>1, exhaustive strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female:male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female:male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female: male ratio of expression in S. japonicum divided by female: male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns, only genes with TPM >1 were used.

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Figure 2—figure supplement 7. Adult expression patterns (TPM>0, exhaustive strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) *S. mansoni* females, (B) *S. mansoni* males, (C) *S. mansoni* female:male, (D) *S. japonicum* females, (E) *S. japonicum* males, (F) *S. japonicum* female:male, (G) Female expression in *S. japonicum* divided by female expression in *S. mansoni*, (H) Male expression in *S. japonicum* divided by male expression in *S. mansoni*, (I) female:male ratio of expression in *S. japonicum* divided by female:male ratio of expression in *S. mansoni*. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p*-value<0.05, **p*-value<0.001, ***p*-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns, only genes with TPM >0 were used.

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Figure 2—figure supplement 8. Schistosomula expression patterns (RPKM>1, exhaustive strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female: male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female: male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female: male ratio of expression in S. japonicum divided by female: male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns, only genes with RPKM >1 were used.

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Figure 2—figure supplement 9. Schistosoma expression patterns (RPKM>0, exhaustive strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female:male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female:male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female:male ratio of expression in S. japonicum divided by female:male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns, only genes with RPKM >0 were used.

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Figure 2—figure supplement 10. Schistosomula expression patterns (RPKM>1, stringent strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female:male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female:male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female:male ratio of expression in S. japonicum divided by female:male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes previously mapped to the ZW linkage group were assigned to each Z-chromosome stratum based on their coverage patterns (stringent classification); only genes with RPKM >1 were used.

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Figure 2—figure supplement 11. Schistosomula expression patterns (RPKM>0, stringent strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) *S. mansoni* females, (B) *S. mansoni* males, (C) *S. mansoni* female: male, (D) *S. japonicum* females, (E) *S. japonicum* males, (F) *S. japonicum* female: male, (G) Female expression in *S. japonicum* divided by female expression in *S. mansoni*, (H) Male expression in *S. japonicum* divided by male expression in *S. mansoni*, (I) female: male ratio of expression in *S. japonicum* divided by female: male ratio of expression in *S. mansoni*. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p*-value<0.05, **p*-value<0.001, ***p*-value<0.0001). Genes previously mapped to the ZW linkage group were assigned to each Z-chromosome stratum based on their coverage patterns (stringent classification); only genes with RPKM >0 were used.

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Figure 2—figure supplement 12. Schistosoma expression patterns (RPKM>1, exhaustive strata, Wormbase orthologs) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female:male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female:male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female:male ratio of expression in S. japonicum divided by female:male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns; only genes with RPKM >0 were used. This figure differs from Figure 2—figure supplement 8 as the Wormbase Parasite list 1:1 orthologs was used instead of our own reciprocal best hit results.
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Figure 2—figure supplement 13. Schistosomula expression patterns (TPM>1, exhaustive strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female: male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female: male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female: male ratio of expression in S. japonicum divided by female: male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns, only genes with TPM >1 were used.

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Figure 2—figure supplement 14. Schistosomula expression patterns (TPM>0, exhaustive strata) of genes located in the different strata of the Z (S0, S1man and S1jap), as well as pseudoautosomal and autosomal genes. The distribution of expression values is shown for (A) S. mansoni females, (B) S. mansoni males, (C) S. mansoni female:male, (D) S. japonicum females, (E) S. japonicum males, (F) S. japonicum female:male, (G) Female expression in S. japonicum divided by female expression in S. mansoni, (H) Male expression in S. japonicum divided by male expression in S. mansoni, (I) female:male ratio of expression in S. japonicum divided by female:male ratio of expression in S. mansoni. Asterisks represent levels of significance of comparisons to the control autosomal genes (*p-value<0.05, **p-value<0.001, ***p-value<0.0001). Genes were assigned to each Z-chromosome stratum based only on their coverage patterns, only genes with TPM >0 were used.

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Figure 2—figure supplement 15. Z-linked and autosomal female: male ratio of gene expression using different filters. The Z-linked and autosomal gene expression patterns are shown in S. japonicum and S. mansoni. Different filters were applied: a minimum threshold of expression of 1 RPKM in all libraries (A–D), a minimum threshold of expression of 3 RPKM in all libraries (E–H), or a minimum threshold of expression of 1 RPKM per stage (as in the main manuscript), together with a filter on fold change to account for strong sex-biases (FC <2 for female: male ratio and male: female ratio) (I–L). Z refers to the female: male ratio of expression in the Z-specific region and A refers to the female: male ratio of expression on autosomes. The level of significance of each comparison is denoted with asterisks: ***p-value<0.0001.
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Figure 2—figure supplement 16. Z-linked and autosomal gene expression in females and males using different filters. The Z-linked and autosomal gene expression patterns are shown for *S. japonicum* and *S. mansoni*. Different filters were applied: a minimum threshold of expression of 1 RPKM in all libraries (A–D), a minimum threshold of expression of 3 RPKM in all libraries (E–H), or a minimum threshold of expression of 1 RPKM per stage (as in the main manuscript), together with a filter on fold change to account for strong sex biases (FC <2 for female:male ratio and male:female ratio) (I–L). Fem-Z and Male-Z refers to the female: male ratio of expression in the Z-specific region and Fem-A and Male-A refers to the female: male ratio of expression on autosomes, in female and male, respectively. The level of significance of each comparison is denoted with asterisks: *p-value < 0.05, **p-value < 0.001, ***p-value < 0.0001.

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Figure 2—figure supplement 17. Z-linked and autosomal female:male ratio of gene expression according to presence/absence of known protein-protein interactions. The Z-linked and autosomal gene expression patterns are shown for schistosomula and adults, in *S. japonicum* (A–B) and *S. mansoni* (C–D). We considered only genes with minimum level of expression RPKM >1 in all stages, did not take into account the ancestral state of expression, and used the ‘exhaustive strata’ set of genes. -PPIs and +PPIs refer to the female:male ratio of expression in the lineage-specific Z-linked strata S1jap and S1mans, respectively. The level of significance of each comparison is denoted with asterisks: ***p-value<0.0001.

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Figure 3. Convergent changes in the expression of Z-linked genes in *S. japonicum* and *S. mansoni* after sex chromosome differentiation. The Z-linked and autosomal gene expression patterns (normalized by ancestral pseudoautosomal or autosomal expression, to show changes since the appearance of the two S1 strata) are shown for S1 jap in *S. japonicum* (A-D) and S1 mans in *S. mansoni* (E-F). Fem-S1j and Male-S1j refer to the normalized expression levels of genes in the stratum S1 jap in females and males, Fem-S1m and Male-S1m refer to the normalized expression levels in S1 mans, and Fem-A and Male-A refer to the normalized expression levels of autosomal genes in females and in males, respectively. The level of significance of each comparison (Wilcoxon rank sum test with continuity correction) is denoted with asterisks: *p*-value<0.05, **p*-value<0.001, ***p*-value<0.0001.

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Figure 3—figure supplement 1. Z-linked and autosomal female:male ratio of gene expression, normalized by ancestral autosomal expression, and using different filters. The Z-linked and autosomal gene expression patterns (normalized by ancestral pseudoautosomal or autosomal expression, to show changes since the appearance of the two S1 strata) are shown for S1jap in *S. japonicum* and S1mans in *S. mansoni*. Different filters were applied: a minimum threshold of expression of 1 RPKM in all libraries (A–D), a minimum threshold of expression of 3 RPKM in all libraries (E–H), or a minimum threshold of expression of 1 RPKM per stage (as in the main manuscript), together with a filter on fold change to account for strong sex biases (FC<2 for female:male ratio and male:female ratio) (I–L). S1jap and S1mans refer to the female:male ratio of expression in the lineage specific Z-linked strata S1jap and S1mans, respectively. The level of significance of each comparison is denoted with asterisks: ***p-value<0.0001.

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Figure 3—figure supplement 2. Z-linked and autosomal gene expression in females and males, normalized by ancestral autosomal expression, and using different filters. The Z-linked and autosomal gene expression patterns (normalized by ancestral pseudoautosomal or autosomal expression, to show changes since the appearance of the two S1 strata) are shown for S1 jap in *S. japonicum* and S1 mans in *S. mansoni*. Different filters were applied: a minimum threshold of expression of 1 RPKM in all libraries (A–D), a minimum threshold of expression of 3 RPKM in all libraries (E–H), or a minimum threshold of expression of 1 RPKM per stage (as in the main manuscript), together with a filter on fold change to account for strong sex biases (FC <2 for female: male ratio and male: female ratio) (I–L). Fem-S1j and Male-S1j refer to the normalized expression levels of genes in the stratum S1 jap in females and males, Fem-S1m and Male-S1m refer to the normalized expression levels in S1 mans, and Fem-A and Male-A refer to the normalized expression levels of autosomal genes in females and in males, respectively. The level of significance of each comparison is denoted with asterisks: *p*-value<0.05, **p*-value<0.001, ***p*-value<0.0001. 

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Figure 4. Transcript and protein dosage of Z-linked and autosomal genes in *S. mansoni* heads and gonads. (A), (B) The female:male (F:M) ratio of protein dosage in *S. mansoni* heads (A) and gonads (B), for Z-specific (Z), pseudoautosomal (PSA) or autosomal (A) genes. The dotted line shows the autosomal median of F:M expression. The level of significance of each comparison (Wilcoxon rank sum test with continuity correction) is denoted with asterisks: *p-value<0.05, **p-value<0.001, ***p-value<0.0001. (C), (D) Pearson correlation between the female:male ratio of expression obtained by proteomics (y-axes) and by microarrays (x-axes) in *S. mansoni* heads (C) and gonads (D). A positive correlation (coefficients ρ) is observed for Z-linked (Z, in orange), pseudoautosomal (PSA, in grey) and autosomal genes (A, in darkgrey). The level of significance of each correlation is denoted by asterisks: *p-value<0.05, **p-value<0.001, ***p-value<0.0001, N.S. p-value>0.05. No significant difference was found between the correlation obtained for Z-linked and autosomal genes in either tissue (using a Fisher r-to-z transformation).

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Figure 4—figure supplement 1. Pearson correlations between gene dosage at the transcript and protein levels in male heads and gonads. A positive correlation (coefficients R) is observed for Z-linked (Z, in light blue), pseudo-autosomal (PSA, in grey) and autosomal genes (A, in dark blue). The level of significance of each correlation is denoted by asterisks: *p-value<0.05, **p-value<0.001, ***p-value<0.0001. No significant difference was found between the correlations obtained for Z-linked and autosomal genes in either tissue (using a Fisher r-to-z transformation).

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Figure 4—figure supplement 2. Pearson correlations between gene dosage at the transcript and protein levels in female heads and gonads. A positive correlation (coefficients R) is observed for Z-linked (Z, in light pink), pseudo-autosomal (PSA, in grey) and autosomal genes (A, in dark pink. The level of significance of each correlation is denoted by asterisks: *p-value<0.05, **p-value<0.001, ***p-value<0.0001. No significant difference was found between the correlations obtained for Z-linked and autosomal genes in either tissue (using a Fisher r-to-z transformation).

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Figure 4—figure supplement 3. Pearson correlations between the female: male ratio of expression obtained by proteomics (y-axes) and by microarrays (x-axes) in S. mansoni heads and gonads, using only genes with male-biased expression in the microarray data. A positive correlation (coefficients R) is observed for Z-linked (Z, in orange), pseudo-autosomal (PSA, in grey) and autosomal genes (A, in darkgrey). The level of significance of each correlation is denoted by asterisks: *p-value<0.05, **p-value<0.001, ***p-value<0.0001, N.S. p-value>0.05. No significant difference was found between the correlations obtained for Z-linked and autosomal genes in either tissue (using a Fisher r-to-z transformation).

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Appendix 1—figure 1. Determination of Z-specific maximum coverage threshold for S. mansoni reference species.

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Appendix 1—figure 2. Determination of Z-specific maximum coverage threshold for *S. japonicum* species.

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Appendix 1—figure 3 Determination of Z-specific maximum coverage threshold for S. haematobium species.
DOI: https://doi.org/10.7554/eLife.35684.050
Appendix 1—figure 4. Correlation analysis between RNAseq libraries: heatmaps.
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