Repeated Parallel Evolution of Minimal rRNAs Revealed from Detailed Comparative Analysis

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Abstract

The concept of a minimal ribosomal RNA-containing ribosome, a structure with a minimal set of elements capable of providing protein biosynthesis, is essential for understanding this fundamental cellular process. Nematodes and trypanosomes have minimal mitochondrial rRNAs and detailed reconstructions of their secondary structures indicate that certain conserved helices have been lost in these taxa. In contrast, several recent studies on acariform mites have argued that minimal rRNAs may evolve via shortening of secondary structure elements but not the loss of these elements as shown for trypanosomes and nematodes. Based on extensive structural analysis of chelicerate arthropods, we demonstrate that extremely short rRNAs of acariform mites share certain structural modifications with nematodes and trypanosomes: loss of helices of the GTPase region and divergence in the evolutionarily conserved connecting loop between helices H1648 and H1764 of the large subunit rRNA. These highly concerted parallel modifications indicate that minimal rRNAs were generated under the strong selection that favored or tolerated reductions of helices in particular locations while maintaining the functionality of the rRNA molecules throughout evolution. We also discuss potential evolution of minimal rRNAs and atypical transfer RNAs.

Key words: acariform mites, Dermatophagoides farinae, GTPase region modifications, acariform mites, house dust mites, Dermatophagoides farinae, minimal mitochondrial rRNA

As part of the ribosome, large and small subunit ribosomal RNA molecules (l-, s-rRNA) and numerous ribosomal proteins play a crucial role in the fundamental processes of translation and protein biosynthesis (Green and Noller 1997; Agrawal et al. 2000; Carter et al. 2000; Nissen et al. 2000). The concept of a “minimal ribosome,” a structure with a minimal set of elements capable of maintaining functionality (Mears et al. 2002; Mushegian 2005), is essential for understanding these important ribosomal functions and can help answer questions about the ribosome’s evolution (Hury et al. 2006; Smith et al. 2008). It is interesting that proteins constituting minimal ribosomes may be substantially divergent in terms of length, amino acid composition, and function. For example, some ribosomal proteins have C-terminal extensions compensating for the reduced functional rRNA components, or a protein may be modified to functionally substitute another protein (Mushegian 2005; Zikova et al. 2008; Ayub et al. 2009). Shortening and modifications of rRNA itself have received more attention (Mears et al. 2002; Sharma et al. 2009). “Minimal” rRNAs lack several typical structural elements characteristic of the rRNAs found elsewhere in a particular phylogenetic lineage and approach the minimal level of simplicity necessary for a functional translational system (Sharma et al. 2009). Note that rRNAs may display significant shortening and loss of helices without attaining the minimal level of simplicity (e.g., bacteria vs. mammals) (Suzuki et al. 2001a, 2001b; Sharma et al. 2003; Smits et al. 2007), thus, representing an example of reductive evolution (e.g., Kurland et al. 2007).

So far, minimal rRNAs (as defined by the secondary structure and length) have been found only in nematodes and trypanosomes, with the simplest rRNA structures occurring in nematodes. Computational (Gutell and Fox 1988; Cannone et al. 2002; Mears et al. 2002; Sharma et al. 2009) and experimental (Sharma et al. 2009) evidence elucidating which structural elements have been highly conserved evolutionarily (and, thus, functionally important) has been presented for these taxa. Interestingly, l-rRNAs of these 2 phylogenetically distant groups share striking structural similarities: the absence of certain helices of the GTPase region (e.g., H837, H946), destabilization of helix H1648, and divergence of a connecting loop flanking H1648. In Archaea, bacteria, and the majority of eukaryotes, these helices and the conserved loop are normally present.
is interesting that a potential similarity in the secondary structure of l-DNA of nematodes with that of a spider was briefly noted previously (Masta 2000), although without reconstructing the 5’-half of the molecule including the GTPase region.

In contrast to these studies, several recent works on acariform mites have argued that minimal rRNAs may evolve via simple shortening and have one of the shortest mitochondrial rRNAs. This aspect of the work also tests whether the dramatic changes associated with minimal rRNAs, especially in size in minimal rRNAs is accounted for by the GTPase region of l-rRNA of trypanosomes and nematodes.

In order to determine whether extremely short rRNAs in certain arachnids evolved via loss of structural elements or by overall shortening, we conduct a thorough comparative structural analysis of chelicerate rRNAs focusing on acariform mites, which have one of the shortest mitochondrial rRNAs. This work also tests whether the dramatic changes associated with minimal rRNAs, especially the GTPase region of l-rRNA, are exclusive to these groups.

### Materials and Methods

#### Sequences

Sequences corresponding to the mitochondrial large and small subunit rRNA of 43 chelicerate taxa (see Supplementary Data S1 and S2) were downloaded from GenBank. The accuracy of the original inference of gene boundaries (e.g., if they included transfer RNAs [tRNAs]) was checked, and sequences representing *Dermatophagoides pteronyssinus* (GenBank: NC_012218), *Steganacarus magus* (NC_011574), and *Varroa destructor* (NC_004454) were corrected. We sequenced the entire mitochondrial genome of the American house dust mite, *Dermatophagoides farinae* (GQ465336), and obtained sequences of the region corresponding to s-rRNA, tRNA-Val, l-rRNA for an additional 4 species (*Gymnopus longior* [GQ465344], *G. osu* [GQ465345], *Sternothophagus bakeri* [GQ465343], and *Santacassia* sp. [GQ465346]) (Klimov and O'Connor 2009). We amplified the mitochondrial genome in several large fragments using arachnid specific primers and then sequenced these fragments via primer walking. The variable-length control region was cloned, and 6 clones were sequenced to include all observed extremities in size (for details, see Klimov and O'Connor [2009]).

#### Inference of rRNA Secondary Structure

The helix numbering system for *Escherichia coli*, as adopted on the comparative RNA web (CRW) (Cannone et al. 2002), was used, and we also use the sequential numbering system (e.g., Sharma et al. 2009) in tables and figures to facilitate comparison. Secondary structure of acariform mites and other chelicerates (see S1, S1: secondary structure alignments for l- and s- rRNA, respectively) was inferred with reference to the rRNA structure of *Drosophila melanogaster* (U37541) and *D. virilis* (X50591), representing a typical rRNA structure, and *Caenorhabditis elegans* (X54252), as a representative minimal rRNA structure. Both the secondary structure diagrams and global alignment are available for these taxa (Cannone et al. 2002). The inclusion of *Limulus polyphemus* (NC_003057), a basal chelicerate showing substantial sequence similarity with *Drosophila*, was especially useful to confirm the structure of certain divergent regions.

Alignment and helix annotation was done in MacClade (Maddison DR and Maddison WP 2005). The program XRNA (Weiser and Noller 2010) was used to visualize secondary structures. MacClade helix annotations (see S1, S2: annotated alignments) were converted to the XRNA format in MS Excel.

For a broad characterization of conservation and divergence and to confirm that the loss of specific helices that typify minimal rRNAs do not occur in other taxa, our structural alignment of chelicerate taxa was compared with an independent extensive alignment of mitochondrial rRNA from the CRW site (Cannone et al. 2002), including 899 and 285 taxa for s- and l-rRNA, respectively.

There is no agreement on whether domain III of l-rRNA is present in Chelicerata (Fahrlein et al. 2009; Masta 2010) or even in Nematoda (Lavrov and Brown 2001; Mears et al. 2002; He et al. 2005). No data showing that putative helices of this domain display compensatory mutations were presented (He et al. 2005; Masta 2010), and we were unable to confirm these structures using our structural alignment. In this study, we followed the results of an extensive comparative analysis suggesting that this domain is probably absent in Chelicerata (Cannone et al. 2002). Similarly, for the arachnid *Phalangium opilio*, a very elaborated structure for domain I of l-rRNA has been proposed (Masta 2010) without demonstrating compensatory mutations.

### Length Analysis of Mitochondrial rRNA Sequences Deposited in GenBank

Sequences of the mitochondrial rRNA genes deposited in GenBank may be misleading because inference of their 5’ and 3’ ends is difficult without experimental data. However, even if a portion of wrongly annotated GenBank sequences is present, this analysis still can be useful (given the absence of any similar analysis) as soon as the potential presence of inaccuracies is realized. Here, we present this analysis as a separate part of our study to identify potential minimal rRNAs and draw attention to problematic sequence annotations. Our main conclusions are independent from inaccuracies in deducing rRNA ends. The major reduction in size in minimal rRNAs is accounted for by the GTPase region (Table 1), which is located in the middle of the 5’ half of l-rRNA and is clearly identifiable in arachnids (Supplementary Figure S3).

Negatively biased inaccuracies in deducing rRNA ends may be identified by the presence of noncoding regions which may contain the real end of rRNA genes, introns, intergenic spacers, or control regions (assuming that gene boundaries of adjacent genes are accurate, which is true in many cases). Mitochondrial DNA usually does not have long intergenic noncoding regions (except for the easily...
identifiable control region). That is why a short rRNA gene surrounded by long noncoding regions (as annotated in GenBank) should be treated as suspect. At this point, reporting the length of noncoding regions adjacent to an rRNA gene (as annotated in GenBank) will indicate potential uncertainty in deducing its length.

The standalone version of the program FeatureExtract 1.2 (gb2tab-1.2.1) (Wernersson 2005) was used to extract spliced rRNA sequences (-f rRNA -s) from mitochondrial genomes deposited in GenBank. Annotations without an explicit “join” statement were corrected manually, whereas records containing other obvious annotation errors were excluded. The output was further processed in MS Excel to structure the information by gene type (s- or l-rRNA), length, and taxonomy. Sequences with extremely short rRNA as deposited in GenBank were further validated using the curated mitochondrial genome database (Lupi et al. 2010), and adjacent noncoding regions were recorded.

Results

Comparative Analysis of the Large Subunit Mitochondrial rRNA

All the losses of the large subunit rRNA that are shared between *Leishmania tarentolae* and *C. elegans* (minimal rRNA taxa) have also been detected in mites (Figure 1), identifying the evolution of minimal rRNAs in these groups. These losses (Table 2) are the: 1) loss of an evolutionarily conserved connecting loop (containing the sequence AAYTCRG-CAA) between helices H1648 and H1764 of l-rRNA, 2) destabilization of helix H1648 (i.e., the complement to its 3’ part is not evident), and 3) absence of large helices, presumably H822 and H837, of the GTPase region. This last loss accounts for one of the major size reductions in the large subunit of the minimal rRNA (116.1 ± 26.0 nucleotides shorter than the typical large subunit; Table 1). An extensive comparative analysis indicates that the loss of the small helix H1183 (Table 2) is not limited to the evolution of minimal rRNAs. However, this loss is rare among other taxa (e.g., the protozoan *Plasmodium*, sea lilies and feather stars (Crinoidea), the acorn worm *Balanoglossus*, and several gastropods). Likewise, H837 was lost in only one taxon without the other concerted structural losses that characterize a minimal rRNA (a stylommatophoran gastropod [Lydeard et al. 2000]).

In contrast to nematodes and trypanosomes, in which minimal rRNAs are present in all the constituent taxa, both minimal and typical rRNAs are represented in the different chelicerate taxa. In particular, typical rRNAs are found in the exemplar taxa *Limulus* (a horseshoe crab) and *Ixodes* (a tick), despite the evolution of minimal rRNAs in *Habronattus*

Table 1 Variation in the mitochondrial large subunit rRNA length, its GTPase region, and the evolutionary Conserved loop in selected taxa with typical and minimal rRNAs

<table>
<thead>
<tr>
<th>Taxa with typical rRNAs</th>
<th>GenBank</th>
<th>l-rRNA</th>
<th>GTPase regiona</th>
<th>Differenceb</th>
<th>Conserved loopc</th>
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<td><em>Drosophila melanogaster</em></td>
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<td>4.6 ± 12.64</td>
<td>10.9 ± 4.07</td>
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<tr>
<th>Taxa with minimal rRNAs</th>
<th>GenBank</th>
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<th>GTPase regiona</th>
<th>Differenceb</th>
<th>Conserved loopc</th>
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<td>1000</td>
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<td>232</td>
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<td>221.9 ± 25.99</td>
<td>-116.1 ± 25.99</td>
<td>72 ± 15.24</td>
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</table>

a Length is measured from the 3’ end of helix H671 to the 5’ end of helix H1764. This includes the GTPase region (helices H837–H1030, H1164) and its adjacent regions.
b Difference (%) of the sequence AACUAGGCAAA (length always constant) in the connecting loop located between helices H1648 and H1764 of l-rRNA.
c The presence of domain III in trypanosomes (minimal rRNA taxa) makes comparisons incompatible with other taxa (without domain III). Thus, the length without domain III is given (the full length is indicated in parenthesis). Extensive comparisons across eukaryotic lineages are available at the CRW Web site.
d Length, as appears in GenBank, is corrected to exclude tRNA-Val.
e Length, as appears in GenBank, is corrected to exclude tRNA-Lys.
(a jumping spider), *Dermatophagoides* (a house dust mite), and other acariform mites (Table 2).

**Comparative Analysis of the Small Subunit Mitochondrial rRNA**

In contrast to the losses described above for the large subunit rRNA, the changes specific to the small subunit rRNA are not all shared between nematodes and trypanosomes or exclusive to taxa with minimal rRNAs. However, there are some remarkable commonalities between the nematode and the arachnid taxa having pronounced shortening of s-rRNA (Figure 2, Table 3), suggesting some functional association with the evolution of the minimal rRNA. Moreover, these losses are not evident in most taxa with typical rRNA based on the CRW data set including 899 other taxa. The shared changes between nematodes and acariform mites with minimal rRNAs include the 1) loss of helix H47 (which is present in trypanosomes and many typical RNA taxa, except for *Ixodes*, but absent in *Plasmodium*, which possesses a highly...
Table 2  Characterization of the helices of the mitochondrial large subunit rRNA that have been lost across taxa (marked with an X), and identification of losses that are specific to and shared among minimal rRNA taxa; taxa with minimal rRNAs are shown in bold, and helices that do not exhibit evolutionary changes are not listed

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<th>H183</th>
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<th>H812</th>
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* Helix numbering system follows that of the CRW for *Escherichia coli* (Cannone et al. 2002); sequential helix numbering system (second row) was also used to facilitate comparison (e.g., Sharma et al. 2009). Helices not exhibiting evolutionary changes are H563, H589, H671, H687, H736, H777, H1057, H1072, H1087, H1196, H1764, H1775, H1782, H1792, H1830, H1835, H1906, H1925, H1935, H2023, H2043, H2064, H2077, H2246, H2455, H2507, H2520, H2547, H2588, and H2646.

* A large fragment between helices H671 and H1764 is reduced and very divergent in minimal rRNA taxa. From canonical helices H822, H837, H946, only one short helix remains.

* Domain III in *L. tarentolae* includes helices H1295, H1303, H1345, and H1385.

* Leptotrombidium pallidum, *L. akamushi*, *L. deliensis*.

* Dermatophagoides farinatus, *D. pteronyssinus*, *Gymnoglyphus longior*, *Stenophagoides bakeri*.
Figure 2. Secondary structure of the mitochondrial small subunit rRNA of the mite *Dermatophagoides farinae* superimposed upon the schematic representation of typical rRNA of *Drosophila melanogaster* (shown as outline). Helix numbering system as on Figure 1.
Table 3  Characterization of the helices of the mitochondrial small subunit rRNA that have been lost across taxa and identification of losses (marked with an X); taxa with minimal rRNAs are shown in bold, and helices that do not exhibit evolutionary changes are not listeda

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* Dermatophagoides farinae, D. pteronyssinus, Gymnoglyphus longiseta, Sturaphagoides harkeri.

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a Helix numbering system follows that of the CRW for *Escherichia coli* (Cannone et al. 2002); sequential helix numbering system (second row) was also used to facilitate comparison (e.g., Sharma et al. 2009). Helices not exhibiting evolutionary changes: H500, H511, H673, H769, H885, H921, H939, H944, H960, H984, H1047, H1350, H1399, and H1506.

b Also includes helices H113, H122, and H316.
c Also includes helices H984, H1047, H1068, H1074, and H1113.

d *Leptotrombidium pallidum, L. akamushi, L. deliens*

e *Dermatophagoides farinae, D. pteronyssinus, Gymnoglyphus longiseta, Sturaphagoides harkeri.*
Our results (Table 1) agree with those published previously in trypanosomes and many typical rRNA taxa but absent in Plasmodium, 2) destabilization of helix H367 (which is present in trypanosomes and many typical rRNA taxa but absent in Plasmodium), 3) destabilization of helices H17, H27, H39, H577, H655, and H722 (present in trypanosomes) and deviation from the canonical secondary structure, and 4) destabilization of helix H567 (which is absent or destabilized in trypanosomes, as well as in certain dasyuromorphid marsupials and in a squid, among other taxa; note inferences about this helix are difficult because of the small size, 4 bp).

Length Analysis of Animal Mitochondrial rRNA

The shortest s-rRNA (513 nt) was detected in an acanthocephalan (NC_006892), whereas the longest (2036 nt) was found in the placozoan, Trichoplax adhaerens (NC_008151). The length range for l-rRNA is 529 and 3487 nt for a bdelloid rotifer (NC_013568) and the marine sponge, Ainctyrella corregata (NC_006894), respectively.

In the reference minimal RNA taxon C. elegans, the length of s- and l-rRNA is 697 and 953 nt, respectively, whereas for all nematodes, which apparently have the same rRNA secondary structure (Cannone et al. 2002), these values range between 569 and 724 nt (s-rRNA) and 729 and 978 nt (l-rRNA). Using the upper limits in these ranges as cutoff values, an array of potentially minimal rRNA taxa emerges: bdelloid rotifers, Acanthocephala, Platyhelminthes, and some (but not all) Bryozoa, Tunicata, Mollusca, Crustacea, and Chelicerata (Supplementary Table S5). This excludes taxa where the ends of rRNA should be verified as they may be actually situated in large adjacent noncoding regions, for example, Anthozoa (Supplementary Table S5). Overall, there is a nearly continuous distribution of rRNA lengths (Supplementary Figure S4) with higher frequency of length corresponding to either taxa with “short” (e.g., Acanthocephala, Nematoda) or typical rRNA (e.g., Crania, Hexapoda).

Discussion

Reevaluation of Previous Data

Our results (Table 1) agree with those published previously for taxa with the length of l-rRNA and most of the l-rRNA GTPase region similar to those of Drosophila, for example, tick Ixodes hexagonus (Cannone et al. 2002), amblypygid Damon diadema (Fahrlein et al. 2009), and opilionid P. opilio (Masta 2010). However, we found that previously published secondary structures for taxa where l-rRNA length approaches that of model minimal rRNA taxa (Table 1) are highly suspect, for example, Leptotrombidium pallidum (Shao et al. 2006), Panonychus citri (Yuan et al. 2010), S. magnus (Domes et al. 2008), and D. pteronyssinus (Dermaw et al. 2009). In these published secondary structure reconstructions, there was no agreement in regard to the middle portion of the 3′-half of the l-rRNA with several universally conserved helices (e.g., H563, H671, and H777). These universally conserved helices are situated in regions of high sequence conservatism and easily detectable when a large chelicerate data set is used (Supplementary Figure S3). Errors in inference of these helices in these studies entails erroneous inference of the entire GTPase region which is situated immediately downstream of these helices.

Several other studies were not informative in regard to the GTPase region because they only presented incomplete l-rRNA structures such as its conserved 3′-half, for example, tick Haemaphysalis sulcata (Black and Piesman 1994), and spiders Habronattus ornatus (Masta 2000) and Cupiennius salei (Huber et al. 1993).

Minimal rRNAs in Acariform Mites

Detailed structural analyses of extremely short mitochondrial rRNAs are only available for trypanosomes (Sharma et al. 2009) and nematodes (Mears et al. 2002). These studies revealed that these organisms possess the minimal set of secondary structure elements necessary to maintain functionality and applied the term minimal rRNA. However, recent studies in acariform mites (Shao et al. 2006; Domes et al. 2008; Dermaw et al. 2009; Yuan et al. 2010) cast doubts on this conclusion and suggest that extremely short rrRNAs may not have been generated by simple overall shortening, without modifications in secondary structure. We reanalyzed these mite secondary structures and found that they are highly suspect, given that even universally conserved helices (e.g., H563, H671, and H777 of l-rRNA) were inferred incorrectly and cannot be confirmed using our extensive chelicerate data set (Supplementary Figure S3). In contrast to these studies, we found that the l-rRNA secondary structure in all acariform mites and a jumping spider (Habronattus sp.) is very similar to that of trypanosomes and even more similar to that of nematodes. The similarities include significant overall shortening of the GTPase region, loss of its large helices (H822 and H837), and extreme divergence of the conserved connecting loop situated between helices H1648 and H1764 (Table 1). Interestingly, other chelicerates retain the typical RNA structure (e.g., ticks, horse-shoe crabs, harvestmen, amblypygids, solifugids, and ricinuleids).

Phylogenetic affinities of acariform mites within Chelicerata are not fully understood. As many as 10 chelicerate orders have been considered as their sister groups, although with strong conflicts among alternative hypotheses based either on morphology or DNA sequences (reviewed in Krantz 1978; Dunlop and Arango 2005; Dunlop and Alberti 2008; Pepato et al. 2010). Given that sister group relationships of acariform mites and spiders are unlikely (e.g., Pepato et al. 2010; Regier et al. 2010), minimal rRNAs of spiders probably evolved independently from those of acariform mites.

The discovery of structurally similar minimal rRNAs in mites and spiders demonstrates that these concerted changes (Figures 1 and 2) have occurred independently and repeatedly in trypanosomes, nematodes, and a subset of arachnids, suggesting that the dramatic evolutionary changes associated with minimal rRNAs occurred under the strong selection to maintain functionality of the molecule. Thus, evolution of the minimal RNA could represent either 1) an adaptive slope...
where mutation pressure causes overall shortening of mitochondrial genomes (e.g., Mira et al. 2001), including rRNA and purifying selection does not allow changes in rRNA structure disruptive to the basic functioning of the ribosome or 2) a new adaptive peak, where the minimal ribosome functions more efficiently or/and the small gene size gives selective advantages due to faster replication or energy savings (Maniloff 1996; Selosse et al. 2001). Currently, there are no available experimental data indicating that minimal ribosomes are more efficient, and the replication advantage hypothesis has been contested (e.g., Mira et al. 2001). Hypothesis 1) seems to be more likely because there is no discontinuity in the rRNA length across animals, and there are taxa showing somehow intermediate secondary structures between minimal and typical rRNA, for example, similar reduction of the GTPase center of l-rRNA (H837) was demonstrated for stylommatophoran gastropods (land snails) (Lydeard et al. 2000). When viewed in this framework, the variation observed in the structure of s-rRNA of taxa with minimal rRNAs (Table 3) highlights the different evolutionary trajectories across taxa during the minimization of their rRNAs.

The phenomenon of extreme shortening of rRNA may not be restricted to nematodes, trypanosomes, and certain arachnids and may be much more widespread in animals than previously recognized (Supplementary Table S5). Extremely short mitochondrial rRNAs have been documented in scattered literature accounts for bdelloid rotifers (Min and Park 2009), acanthocephalans (Steinauer et al. 2005), copepods (Crustacea) (Machida et al. 2002; Tjensvoll et al. 2005; Burton et al. 2007), or simply available as GenBank submissions (DeJong et al. 2004; e.g., Gissi et al. 2010; von Nickisch-Rosenegk et al. 2001; Helfenbein et al. 2004; Medina et al. 2006; Waeschenbach et al. 2006; Park et al. 2007; Huyse et al. 2008). Unfortunately, 1) length and boundaries of these genes may not be determined accurately as this requires experimental data and 2) no secondary structure reconstructions were conducted for the majority of these organisms. Thus, it is still unclear if these rRNAs may in fact represent a minimal rRNA. Our study draws attention to these records and indicates the need for a large-scale comparative analysis elucidating the nature of these unusually short rRNAs.

Minimal rRNAs and Atypical tRNAs

We also suggest that there is additional independent evidence for the adaptive context of minimal rRNA evolution—namely, the coevolution of minimal rRNAs and modifications of tRNAs. Wolstenholme et al. (1987) hypothesized that shortening of l-rRNA via loss of secondary structural elements coevolved with the presence of atypical, noncloverleaf tRNAs in nematodes. Later, the same co-occurrence of shortened rRNA and atypical tRNAs was demonstrated for spiders (Masta 2000; Masta and Boothe 2004, 2008; Qiu et al. 2005), acariform mites (Shao et al. 2006; Klimov and O’Connor 2009), bdelloid rotifers (Min and Park 2009), and acanthocephalans (Steinauer et al. 2005). The generality of Wolstenhome et al.’s hypothesis was challenged when both cloverleaf and noncloverleaf tRNAs were detected in the nematode Trichinella spiralis with minimal rRNA (Lavrov and Brown 2001). Even though modified rRNA and tRNAs do not always co-occur, the evolution of modified rRNAs and tRNAs may be linked indirectly by elongation factors (EF-Tu and EF-G). These enzymes bind to the GTPase center of l-rRNA (Spahn and Nierhaus 1998; Wilson and Noller 1998), which is substantially modified in minimal rRNA taxa. Atypical tRNAs are not recognized by EF-Tu which delivers aminoacyl-tRNAs to the ribosome (Ohtsuki et al. 2001, 2002; Arita et al. 2006). Instead, 2 different elongation factors, EF-Tu1 and EF-Tu2, process the modified tRNAs (Ibba 2002; Arita et al. 2006). Additional investigation will be needed to confirm whether evolutionary changes between minimal rRNAs and modified tRNAs, possibly mediated by the interactions with enzymes involved in translational processes, have indeed occurred in a concerted fashion. Such information could provide intriguing evidence of the underlying adaptive context for the repeated evolution of minimal rRNAs documented here.

Supplementary Material

Supplementary material can be found at http://jhered.oxfordjournals.org/

Funding

US National Science Foundation (DEB-0613769); Russian Ministry of Education and Science (02.740.11.5139).

Acknowledgments

We thank Tim Connallon, George Hammond, and Ellen Foot for helpful comments on the manuscript, Dan Chang and Thomas Duda for assistance with the cloning, and Ellen Foot and Kristen Mar for assistance with molecular laboratory work. The molecular work of this study was conducted in the Genomic Diversity Laboratory of the University of Michigan Museum of Zoology.

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Heptathela hangzhouensis


Rhodonea zopfii (Bdelloidea: Rotifera: Syndermata). BMC Genomics. 10:533.


