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Abstract

The mud snails endemic to the East Atlantic/Mediterranean region (genus *Tritia*; subfamily Nassariinae) account for the second highest diversity within the family Nassariidae (Gastropoda: Buccinoidea). In order to understand how the diversity of species, shell morphologies, and ecological traits evolved within this genus, a robust phylogenetic framework is needed, yet still unavailable due to high levels of homoplasy in shell morphology, the main trait used for their taxonomic classification. Here, the near-complete mitogenomes of 20 species representing more than half of the diversity of *Tritia* were sequenced. All mitogenomes of *Tritia* shared the same gene order, which is identical to the consensus reported for caenogastropods. The reconstructed phylogeny indicates that all analyzed *Tritia* species formed a natural group except *Tritia vaucheri*, which was sister to an early diverging clade within subfamily Nassariinae that includes species of genus *Reticunassa* sister to *Nassarius jacksonianus* and *Nassarius* sp. Within *Tritia*, the Northwest Atlantic species *Tritia obsoleta* was placed as the sister group of three mostly East Atlantic/Mediterranean clades (I-III), prompting the reinstatement of the genus *Ilyanassa*. The latter three clades corresponded to different shell features (I, shell mostly with marked sculpture; II, shell with strong nodules and small size; and III, smooth shell). For *Tritia incrassata*, the analyzed specimens from Norway and from the Spanish Mediterranean coasts showed notable genetic divergence, which may indicate the existence of cryptic species. The ancestral character state reconstruction of protoconch inferred that the ancestor of *Tritia* had planktotrophic larvae, and that a transition to lecithotrophy occurred independently at least three times within Nassariinae. The reconstructed chronogram dated the origin of *Tritia* in the Oligocene and main diversification events during the Miocene to Pleistocene, correlated with drastic shifts in local paleoecosystems caused by cooling events, eustatic sea level changes, and the Messinian Salinity Crisis that favored temperate taxa.

KEYWORDS

Nassariinae, *Tritia*, *Ilyanassa*, mitochondrial genome, phylogeny, chronogram

1. INTRODUCTION

Mud snails or dog whelks (family Nassariidae) are small- to medium-sized snails, readily recognized by their fusiform, slender to broadly ovate shells of moderately sculptured surface (from smooth to cancellate or reticulate) with more or less prominent axial and spiral ribs and cords (Cernohorsky, 1984). The base of the shell aperture has a notch for extension of their long siphon. The columella is short with a pronounced siphonal fold (Cossmann, 1901). The reduced operculum is thin and corneous with a terminal nucleus and often marginally serrated. Most nassariids species are facultative scavengers or non-selective predators (Morton, 2011). Their characteristic long inhalant siphon (as long as their body) together with a well-developed osphradium allows acute chemoreception and efficiently leads to carrion or prey. Their often very wide and flattened foot enables these sea snails to glide quickly and easily over soft substrata.

The nassariids constitute an important component of the biodiversity of tropical and temperate seas and attain their greatest diversity in the tropical Indo-Pacific (Cernohorsky, 1984). A few species have reached the polar seas (Nekhaev, 2014). Mud snails inhabit predominantly in shallow water soft bottoms, but some live in deep water, and many characterize certain types of sediments where they are dominant (Harasewych, 1998; Hayashi, 2004). For instance, the species of the genus *Bullia* are the most conspicuous surfing organisms of the swash zone of many sandy beaches in the southern hemisphere, and some species of *Nassarius* and *Tritia* display dense populations in estuaries and coastal lagoons. Several species have adapted to brackish water and a few have successfully conquered freshwater habitats in Southeast Asia (Strong, Galindo, & Kantor, 2017). Due to their abundance, nassariids have been well studied from different points of view. For instance, many nassarid species are known to accumulate toxins and as such constitute a health problem especially in Asia (Hwang et al., 2005); other species have been used as model organisms, such as *Tritia obsoleta* (as *Ilyanassa obsoleta*) in developmental biology (Goulding & Lindberg, 2016) or *Bullia digitata* in ecological and behavioral studies (Brown, 1980). Furthermore, nassariids have a rich fossil record (Gili & Martinell, 1993, Tracey, Todd, & Erwin, 1993; Haasl, 2000; Harzhauser & Kowalke, 2004; Landau, da Silva, & Gili, 2009) since the lower Cretaceous (Taylor, Morris, & Taylor, 1980) that should help understanding major evolutionary trends within the family when interpreted within a phylogenetic framework.

The first thorough classification of nassariids was based on the shape of the shell columella (Cossmann, 1901), and is still in use with slight modifications (Cernohorsky, 1984). The family was traditionally divided into three subfamilies: Nassarinae, Dorsaniinae and Cylleninae, until Allmon (1990) transferred several genera previously included in Dorsaniinae to establish the new subfamily Bulliinae. However, the taxonomy of these subfamilies, especially the status of genera and

subgenera, has remained far from resolved because of rampant convergence in shell morphology and other phenotypic characters due to adaptations to similar environmental or selective pressures. Moreover, most nassariids species were assigned by default to the genus *Nassarius* and many are still provisionally included in this genus, which demands thorough revision.

Recently, a molecular phylogeny including more than 200 putative nassariid species was reconstructed based on partial sequences of five (mitochondrial and nuclear) genes (Galindo et al., 2016). This molecular phylogeny showed that the morphology-based taxonomy of the family (Cernohorsky, 1984; Allmon, 1990; Haasl, 2000; Kantor, 2003) was dominated by homoplasy and had little phylogenetic significance. Genera were redefined, the new subfamily Buccinanopsinae was created, and the taxon Photinae was reestablished at subfamily level (Galindo et al., 2016).

The reconstructed phylogeny of Galindo et al. (2016) showed that the cosmopolitan subfamily Nassariinae comprises about 80% of nassariid species diversity (MolluscaBase, 2020a). Up to five strongly supported clades were recovered within this subfamily and were assigned to genera with relatively distinct geographical distributions: the Indo-Pacific *Nassarius* and *Reticunassa* (the "*pauper*-complex" *sensu* Kool & Dekker, 2006, 2007, Galindo, Kool, & Dekker, 2017); the mostly Atlantic-Mediterranean *Tritia*; the (East and West) African *Naytia*; and the Caribbean-Panamanian *Phrontis*. Furthermore, these genera showed different types of protoconch. The multispiral protoconchs of species assigned to *Nassarius* and *Reticunassa* have one or two keels, whereas those of species included within *Tritia*, *Naytia*, and *Phrontis* lack a keel (Galindo et al., 2016). Transitions to a paucispiral protoconch have occurred independently within different genera (Galindo et al., 2016).

Phylogenetic relationships among species within the different genera remained largely unresolved in several cases (Galindo et al., 2016). After Galindo et al. (2016) around 60 species were reclassified into genera other than *Nassarius* but more than 300 species remained tentatively in this genus (MolluscaBase, 2020b) awaiting further phylogenetic studies. In this regard, two subsequent mitogenomic studies that focused on the genus *Nassarius* improved the resolution of phylogenetic relationships among species restricted to the China seas (Yang, Li, Kong, & Yu, 2019; Yang et al., 2020), compared with previous attempts based on partial gene sequences (e.g., Zhang & You, 2009; Chen & Zhang, 2012; Pu et al., 2017). As a result of these mitogenomic studies, the composition of the genus *Nassarius* was refined, with *Nassarius jacksonianus* and *Nassarius* sp. (incorrectly identified as *N. acuticostus*; see Supporting Information Figure S1) placed with strong statistical support as sister to *Reticunassa* (Yang, Li, Kong, & Yu, 2019). Furthermore, another mitogenomic phylogenetic study focused on genus *Reticunassa* revealed cryptic species (Yang, Li, Kong, & Yu, 2018). These studies highlight the need of studying in depth the species composition

and phylogenetic relationships within the five recognized Nassariinae genera. They also confirm the high levels of resolution achieved by complete mitochondrial genomes when inferring phylogenetic relationships of gastropods below the family level (Uribe, Puillandre, & Zardoya, 2017).

The traditional taxonomy of the Atlantic/Mediterranean nassariids was mainly based on shell characters, with species classified into different genera (*Hinia*, *Nassarius*, *Sphaeronassa*, *Naytiopsis*, *Cyclope* and *Ilyanassa*). Even though species of *Cyclope* possess rather unique flattened shell geometry, and *Ilyanassa* is restricted to the Northwest Atlantic, the molecular phylogeny of Nassariidae found no evidence to support these genera, which were both synonymized with *Tritia* (Galindo et al., 2016). At present, a total of 40 species are considered valid within *Tritia* (MolluscaBase, 2020c), including four species endemic to the Gulf of Gabès that were recently recognized as valid (Aissaoui, Galindo, Puillandre, & Bouchet, 2017). Several *Tritia* species extend their range distribution to West African coasts living in sympatry with *Naytia* species.

In order to clarify the taxonomy of the genus *Tritia* in the Atlantic/ Mediterranean region, a robust phylogeny of the group is needed. Thus far, only two complete mitochondrial genomes of *Tritia* species are available i.e., *T. obsoleta* (DQ238598; Simison, Lindberg, & Boore, 2006, as *Ilyanassa obsoleta*) and *T. reticulata* (EU827201; Cunha, Grande, & Zardoya, 2009). In the present study, we sequenced the nearly complete (without the control region or partial gene sequences) mitochondrial genomes of 21 specimens representing 20 species of *Tritia* (i.e., half of the diversity of the genus) and of one specimen of the freshwater nassariid *Anentome* sp. as outgroup. Our aims were: (1) to test the monophyly of the genus *Tritia* as currently defined (MolluscaBase, 2020c); (2) to reconstruct robust phylogenetic relationships within the genus; (3) to date the origin and main cladogenetic events during the diversification of this genus; and (4) to test the validity of shell morphology in *Tritia* taxonomy.

2. MATERIALS AND METHODS

2.1. Samples and DNA extraction

The complete list of specimens analyzed in the present study, including their sampling sites, collectors, and museum vouchers is shown in Table 1. Samples were stored in 100% ethanol at 4ºC or -20ºC, and total genomic DNA was isolated from foot muscle using the DNeasy Blood & Tissue Kit (Qiagen, Germany).

2.2. PCR amplification and sequencing

Nearly complete (without the control region or partial gene sequences) mt genomes were amplified in two main steps. First, fragments of *cox1*, *cox3*, *rrnS*, *rrnL*, and *cob* genes were amplified through standard PCRs, which were carried out in a total volume of 25 µl with 1 µl of template DNA (25–40 ng/µl), 2.5 µl of 10× buffer (Mg^{2+} plus), 0.5 µl of dNTPs (2.5 mM), 0.5 µl of each primers (10 µM), 0.2 µl of Taq DNA polymerase (5 U/µl), 0.25µl of BSA (10 mg/ml) and 19.55 µl of DEPC water. The PCR conditions were as follows: an initial denaturing step at 94 °C for 5 min; 40 cycles of denaturing at 94 °C for 60 s, annealing at 39–48°C for 60 s, and extension at 72 °C for 90 s; and a final extension step at 72 °C for 10 min. Standard-PCR products were purified by ethanol precipitation, and Sanger sequenced at Macrogen (Seoul, Korea). Information on standard PCR primers is shown in Supporting Information Table S1.

In the second step, the obtained sequences were used to design specific primer pairs for long PCR amplification of the remaining mitogenome in four fragments (see Supporting Information Table S1). The long PCR reactions contained 2.5 µl of 10× buffer (Mg^{2+} plus), 3 µl of dNTPs (2.5 mM), 0.5 µl of each primers (10 µM), 0.8 µl of template DNA (25–40 ng/µl), 0.2 µl of TaKaRa LA Taq DNA polymerase (5 U/µl), 0.2 µl of BSA (10 mg/ml) and DEPC water up to 25 µl. The following PCR conditions were used: initial denaturing step at 94 °C for 60 s; 45 cycles of denaturing at 98 °C for 10 s, annealing at 53-56 °C for 30 s, and extension at 68 °C for 60 s per kb; final extension step at 68 °C for 10 min. Long PCR products were purified by ethanol precipitation, and fragments from the same mitogenome were pooled together in equimolar concentrations for high-throughput sequencing. For each mitogenome of *Tritia*, a separate indexed library was constructed using the NEXTERA XT DNA library prep Kit (Illumina, San Diego, CA, USA) and run in an Illumina MiSeq platform (2 × 150 paired-end) at AllGenetics (A Coruña, Spain) and NIMGenetics (Madrid, Spain). Among the 20 libraries, five contained also the mitogenomes of cones or buccinoids from different projects (see Supporting Information Table S1).

Due to the degraded condition of the source DNA of *T. ovoidea* and *T. tingitana*, the partial mt genomes of these species were mostly amplified through standard PCRs, as only few long PCRs worked (see Supporting Information Table S1). Those amplified fragments with sizes ≤ 1,000 bp were directly Sanger sequenced with the corresponding PCR primers, whereas the longer PCR products were Sanger sequenced using a primer walking strategy. Sequencing was performed in automated sequencers (ABI PRISM 3700) using the BigDye® Terminator v3.1 cycle-sequencing kit

185 (Applied Biosystems, Foster City, CA, USA), and following the manufacturer's instructions.
186 For some species with tentative identification, namely *N. jacksonianus* and *N. acusticostus*, or
187 of unexpected phylogenetic position, namely *T. ephamilla* and *T. vaucheri*, the barcoding *cox1*
188 fragment was PCR amplified and Sanger sequenced to double check species identity (see
189 Supporting Information Figure S1).
190
191 **2.3. Genome assembly and annotation**
192 The Sanger sequences were assembled using Sequencher 5.0.1. For the specimens from the MNHN
193 collections, some *cox1* sequences were downloaded from Genbank (see Supporting Information
194 Table S1). For Illumina sequence data, the reads corresponding to different individuals were sorted
195 by the corresponding library indices. Raw sequences were analyzed for quality control using
196 FastQC v.0.11.9 (Andrews, 2010), and trimmed and filtered out according to their quality scores
197 using PRINSEQ v.0.20.4 (Schmieder & Edwards, 2011). Assembly of the mitogenomes was
198 performed using Geneious Prime 2019.0.3 (Kearse et al., 2012). The mitogenomes were constructed
199 by repeatedly mapping the original reads (setting a minimum identity of 99%) to the Sanger
200 fragments from the same mitogenome.
201 The newly determined mt genomes were annotated with Geneious Prime 2019.0.3. Annotations
202 of protein-coding genes (PCGs) were defined by setting a limit of 75% nucleotide identity to
203 previously published nassariid mitogenomes (Table 1) in Geneious Prime 2019.0.3, and
204 corroborated using the MITOS Webserver (Bernt et al., 2013) with the invertebrate mitochondrial
205 genetic code. The transfer RNA (tRNA) genes were further identified using tRNA scan-SE 1.21
206 (Schattner, Brooks, & Lowe, 2005) and ARWEN (Laslett & Canbäck, 2008). The ribosomal RNA
207 (rRNA) genes were first identified using the MITOS Webserver (Bernt et al., 2013). The software
208 rendered shorter rRNA genes (due to sequence variability in the ends), and their boundaries were
209 assumed to be between the adjacent genes by comparison with other nassariid mt genomes.
210
211 **2.4. Sequence alignment**
212 The newly sequenced mitogenomes were aligned along with those of other nassariids available in
213 Genbank (Table 1). Representatives of different genera of Nassariinae were included in the ingroup
214 to test the monophyly of *Tritia*. The freshwater nassariid *Anentome* sp. (subfamily Anentominae)

was used as outgroup to root the tree (Galindo et al., 2016). A dataset concatenating the nucleotide sequences of the 13 PCGs and two rRNA genes was constructed and analyzed.

The 13 PCGs were aligned separately guided by amino acid translations (according to the invertebrate mitochondrial genetic code) using Translator X (Abascal, Zardoya, & Telford, 2010), . Nucleotide sequences of the two rRNA genes were aligned separately using MAFFT v7 (Katoh & Standley, 2013) with default parameters. Ambiguously aligned positions were removed using Gblocks v.0.91b (Castresana, 2000) with the following settings: minimum sequence for flanking positions: 85%; maximum contiguous non-conserved positions: 8; minimum block length: 10; gaps in final blocks: no. Finally, the different single alignments were concatenated into a single data set in Geneious Prime 2019.0.3. Sequences were converted into different formats for downstream analyses using DAMBE5 (Xia, 2013).

2.5. Phylogenetic analyses

Pairwise uncorrected *p* sequence distances to delimit species were estimated based on the alignment including the nucleotide sequences of the 13 PCGs and the two rRNA genes. Phylogenetic trees were reconstructed using maximum likelihood (ML; Felsenstein, 1981) and Bayesian inference (BI; Huelsenbeck & Ronquist, 2001). ML analyses were carried out using IQtree 1.6.10 (Nguyen, Schmidt, Von Haeseler, & Minh, 2015) in the CIPRES gateway (Miller, Pfeiffer, & Schwartz, 2010), allowing partitions to have different evolutionary rates (-spp option) and with 10,000 ultrafast bootstrap pseudoreplications (-bb option). BI analyses were performed with MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003), running four simultaneous Monte Carlo Markov chains (MCMC) for 10,000,000 generations, sampling every 1000 generations, and discarding the first 25% generations as burn-in. Two independent runs were performed to increase the chance of adequate mixing of the Markov chains and to increase the chance of detecting failure to converge, as determined by using Tracer v1.6. The effective sample size (ESS) of all parameters was higher than 200. The resulting phylogenetic trees were visualized in FigTree v1.4.2.

The best partition schemes and best-fit substitution models for BI analysis of the data set were determined (see Supporting Information Table S2 for selected best fit partitions and models) using PartitionFinder 2 (Lanfear et al., 2017), under the Bayesian Information Criterion (BIC; Schwarz, 1978). For the 13 PCGs, the partitions tested were: all genes combined; all genes separated (except

atp6-atp8 and *nad4-nad4L*); and genes grouped by subunits (*atp*, *cob*, *cox* and *nad*). Additionally, these three partition schemes were tested considering separately the three codon positions. The two rRNA genes were analyzed with two different schemes (genes grouped or separated). The best-fit substitution models for ML analysis were calculated with ModelFinder (Kalyaanamoorthy, Minh, Wong, Haeseler, & Jermiin, 2017) as implemented in IQ-TREE 1.6.10.

2.6. Ancestral Character State Reconstruction

The type of larval shell or protoconch with a single (paucispiral) or multiple whorls (multispiral) was accessed based on literature (Galindo et al., 2016; Aissaoui, Galindo, Puillandre, & Bouchet, 2017) except for *T. vaucheri*, which was determined by direct examination of the shells (the number of whorls was counted to the nearest quarter whorl; Modica et al., 2020). Both types of protoconch were used as a proxy of the lecithotrophic (direct development using yolk reserves) or planktotrophic (with a feeding veliger phase) modes of larval development (Strathmann, 1978). The evolution of larval development was analyzed by performing an ancestral character state reconstruction in Mesquite v3.6.1 (Maddison & Maddison, 2018) using the Tracing Character History option under ML and mapping onto the identical topology inferred by the ML and BI analyses.

2.7. Estimation of divergence times

The program BEAST v.1.10.4 (Drummond & Rambaut, 2007) was used to perform a Bayesian estimation of divergence times among main nassariid lineages based on PCGs only. An uncorrelated relaxed molecular clock was used to infer branch lengths and node ages. The tree topology was fixed using the identical topology recovered by the ML and BI analyses. For the clock model, the lognormal relaxed-clock model was selected, which allows rates to vary among branches without any *a priori* assumption of autocorrelation between adjacent branches. For the tree prior, a Yule process of speciation was employed. The partitions selected by PartitionFinder 2 (see above) were applied. The final Markov chain was run twice for 100 million generations, sampling every 10,000 generations and the first 10 million were discarded as burn-in, according to the convergence of chains checked with Tracer v.1.6. The effective sample size of all the parameters was above 200.

The posterior distribution of the estimated divergence times was obtained by specifying three

calibration points based on fossil data as priors for divergence times of the corresponding splits. The prior distributions of the three calibration nodes were selected following Ho & Phillips (2009). For the origin of the lineage leading to *T. neritea* and *T. pellucida*, a calibration point was set at the minimum limit of 3.6 million years ago (Mya; exponential distribution, offset: 3.6; mean: 1.0) based on the fossils of *Cyclope migliorinii* that are the oldest for the stem group (Gili & Martinell, 1999; Landau, da Silva, & Grigis, 2009) and dated from the Pliocene (Placenzian; 3.6 - 2.6 Mya) of Spain according to the Paleobiology Database (https://paleobiodb.org). A second calibration point was set at the origin of *Tritia.* A lognormal distribution was applied, with the minimum of 23 Mya and a 95% upper limit of 28.4 Mya (offset: 23; mean: 1.9; standard deviation: 1.9) based on *Nassarius (Hinia) pygmaea* from Germany (Albright et al., 2019) and *Nassarius (Hinia) schlotheimi* from Hungary (Báldi, 1973), both from the Oligocene (Chattian; 28.4 - 23.0 Mya), the oldest Nassariinae fossils in Europe (Lozouet, 1999). A third calibration point was set at the root of the tree. A lognormal distribution was applied, with the minimum of 55.8 Mya and a 95% upper limit of 58.7 Mya (offset: 55.8; mean: 1.0; standard deviation: 1.0) based on the oldest known Nassariinae fossil, which is *Buccitriton sagenum* from the Paleocene (Thanetian; 58.7 - 55.8 Mya) of Lousiana, USA (Glawe, Anderson, & Bell, 2014).

3. RESULTS

3.1. Sequencing and assembly

All newly sequenced mt genomes in the present study lacked the sequences of the *trnF* gene, the control region, and the start of the *cox3* gene because the corresponding fragment could not be PCR amplified. The number of reads, mean coverage, length, and accession number in Genbank of each mitogenome are provided in Table 1. The mt genomes of *T. incrassata*-SP and *T. varicosa* received the minimum (53x; 30,800 reads) and maximum (23,350x; 2,765,768 reads) coverage, respectively (Table 1).

3.2. Genome organization

The newly determined *Tritia* mitogenomes encode for 13 PCGs, two rRNA and 22 tRNA genes (but note that the *trnF* gene could not be determined in all mt genomes; see annotation of each mt genome in Supporting Information Table S3). They all share the same genome organization

described for Caenogastropoda (Osca, Templado, & Zardoya, 2015), with most genes encoded by the major strand and a cluster of tRNA genes (*trnM*, *trnY*, *trnC*, *trnW*, *trnQ*, *trnG*, *trnE*) and the *trnT* gene encoded by the minor strand (Figure 1). All PCGs start with the conventional initiation codon ATG (but note that the start of the *cox3* gene could not be determined in all mt genomes; see Supporting Information Table S3). As for the termination codons, two genes (*cox2* and *atp8*) consistently ended with TAA and two (*nad4L* and *nad5*) stopped with TAG. The incomplete stop codon (TA-), which becomes functional after polyadenylation (Ojala et al., 1981), was observed in all *nad2* genes but that of *Tritia grana*, which ended with TAA. The remaining genes varied in their stop codons depending on the species (Supporting Information Table S3).

3.3. Phylogenetic relationships

Phylogenetic relationships of *Tritia* were reconstructed based on the nucleotide sequences of the concatenated 13 PCGs and two rRNA genes using probabilistic methods (Figure 2). The final matrix was 13,101 positions in length. According to the BIC, the best partition scheme for the PCGs was the one combining genes by subunits but analyzing each codon position separately (Supporting Information Table S2). For the rRNA genes, the best partition scheme was the one combining together *rrnL* and *rrnS* genes. Both ML ($-lnL$= 133,593.77) and BI ($-lnL$= 133,905.39 for run 1; $-lnL$= 133,908.66 for run 2) analyses arrived at identical topologies (Figure 2).

According to the reconstructed phylogeny, *N. jascksonianus* and *Nassarius* sp were recovered closer to *Reticunassa* than to other *Nassarius* species (Figure 2). *Tritia vaucheri* was placed sister to the clade including (*N. jascksonianus* and *Nassarius* sp.) + *Reticunassa*, and apart from the remaining *Tritia* species, which formed a natural group. Within this latter group, the Northwest Atlantic species *T. obsoleta* was placed as sister to three mostly Northeast Atlantic/ Mediterranean clades (I-III). Clade I included ten species distributed into five lineages: (1) *T. ephamilla* (endemic to New Zealand and southern Australia) and *T. ovoidea* + *T. elata*, (2) *T. denticulata*, (3) *T. tingitana*, (4) *T. reticulata* and *T. nitida*, and (5) the "*T. cuvierii* complex" including *T. unifasciata* and *T. cuvierii* + *T. tenuicosta*. This clade was sister to clades II and III (Figure 2). Clade II comprised *T. varicosa* and *T. incrassata* (including one specimen from a Spanish Mediterranean population and one from Norway). Clade III included *T. elongata* + (*T. pallaryana* and *T. corniculum*) sister to a group formed by *T. grana* + (*T. neritea* and *T. pellucida*) and *T. pfeifferi* + *T. mutabilis* (Figure 2).

3.4. Ancestral character state reconstruction

The ancestral character state reconstruction analysis inferred that the Atlantic/Mediterranean nassariids could have originated from an ancestor with a multispiral protoconch, which indicates a planktotrophic mode of larval development (Figure 3). The "*T. cuvierii* complex", clade III, and *T. tingitana* were inferred to represent independent evolutionary transitions to a paucispiral protoconch, suggesting a secondary loss of the planktotrophic mode of larval development to lecitotrophy.

3.5. Divergence times

Main cladogenetic events within *Tritia* were dated using an uncorrelated relaxed molecular clock model, which was calibrated using three Atlantic fossils. The origin of the stem lineage leading to genus *Tritia* (including *T. obsoleta* and without *T. vaucheri*) was dated 24.0 (26.2–23.1, 95% highest posterior density interval, HPD) million years ago (Mya). The first event of diversification within the crown group of *Tritia* was estimated at a mean of 20.4 (23.5–17.1) Mya, separating the Northwest Atlantic *T. obsoleta* from *T. ephamilla* and East Atlantic/ Mediterranean *Tritia* species. The branching of the three main East Atlantic/ Mediterranean clades was estimated to have occurred around 18.9–17.6 (22.0–14.4) Mya. Finally, main diversification events leading to extant *Tritia* species were estimated to have occurred between 16.9–3.9 (20.1–2.0) Mya, whereas divergences of some closely-related species or populations were dated about 0.6–0.1 Mya (Figure 4).

4. DISCUSSION

4.1. Taxonomy of the non-*Tritia* Nassariinae

The often-ornamented shell of nassariids, which could in principle provide numerous characters for taxonomic classification, and had been widely used in the past for this purpose, was found to be prone to convergence at different taxonomic levels (particularly within Nassariinae) when a rather comprehensive molecular phylogeny of the family was inferred (Galindo et al., 2016). This phylogeny provided the long needed scaffold to continue resolving the systematics of the family and opened the way to further phylogenetic studies focusing on relationships within particular clades. Here, we focused on one of these clades, which included nassariinae mostly from the Atlantic/Mediterranean region and was ascribed to genus *Tritia* (Galindo et al., 2016). We

sequenced the near-complete (without the control region or partial gene sequences) mitogenomes of 20 species belonging to *Tritia* and reconstructed a highly resolved phylogeny, which included more than half of the species diversity of this genus (MolluscaBase, 2020c) as well as other nassariinae genera and *Anentome* sp. (subfamily Anetominae) as outgroup.

Within the first offshoot of the tree, *N. jascksonianus* and *Nassarius* sp. were recovered closer to *Reticunassa* than to other *Nassarius*, as previously suggested (Yang, Li, Kong, & Yu, 2019). This is not surprising considering the geographic disparity of the samples and that not all species ascribed to *Nassarius* were included in the molecular phylogeny of the family, impeding proper assignment to clades (Galindo et al., 2016). Given the relative phylogenetic position of the two species and the large uncorrected *p* distance separating them from other clades (16–18%), they could be allocated in a new genus, whose formal description would need a larger taxon sampling and thorough morphological revision beyond the scope of this study.

According to the reconstructed phylogeny, the ascription of *T. vaucheri* to genus *Tritia* was strongly rejected. This taxon was originally described as *Nassa* (*Himia*) *vaucheri* (Pallary, 1906). After examining the syntype of this species, Cernohorsky (1975), transferred it to genus *Chauvetia* (in family Buccinidae). Later, Hoenselaar and Moolenbeek (1988) transferred the species to genus *Nassarius* and designated a lectotype. Finally, the new combination *T. vaucheri* (currently accepted in MolluscaBase, 2020c) was established in a checklist of marine mollusks recorded in Spanish marine waters (Gofas et al., 2017). *Tritia vaucheri* was recovered as an early divergent lineage in the phylogeny, sister to the Indo-Pacific clade (*N. jascksonianus* and *Nassarius* sp.) + *Reticunassa*, although with low statistical support. Hence, this species does not belong to genus *Tritia*, but to another Atlantic genus that is only distantly related and still needs to be determined (*Genus incertae sedis, Gen. inc. sed.*). Therefore, the general shell morphology resemblance of this taxon to other *Tritia* species would represent yet another case of convergence within Nassariidae (Galindo et al., 2016). *Genus incertae sedis vaucheri* is found in the southwestern Mediterranean coasts of Spain and in the nearby Atlantic coasts from south Portugal to Morocco being replaced by *Nassarius argenteus* from Senegal down to the Gulf of Guinea (Gofas, 2011). This latter species was not included in our study but may also belong to the same genus as *Gen. inc. sed. vaucheri*. The above-mentioned distribution is typical of several species of *Tritia* but also of several sympatric species of the African genus *Naytia*. Galindo et al. (2016) provisionally included in this latter genus

N. glabrata (type species), *N. granulosa*, *N. johni*, from West African coasts, and *N. priscardi* from Madagascar, and they highlighted that the members of this genus were characterized by high morphological disparity. The type species and *N. granulosa* exhibit a smooth shell, similar to that of the species of the *Bullia* group, which led Simone & Pastorino (2014) to erroneously include *N. granulosa* in the genus *Bullia*. Conversely, *N. johni* and *N. priscardi*, exhibit a reticulate shell sculpture. *Gen. inc. sed. vaucheri* is quite similar to these two latter species, so it could be possible that it belongs to *Naytia* (the position of this genus in the phylogeny of Galindo et al. 2016 is sister to *Reticunassa*, although with low support). It will be necessary to include mitogenomes of species from other genera (especially from West Africa) into the nassariid phylogeny in order to fully resolve the phylogenetic position of *Gen. inc. sed. vaucheri* and its generic placement.

The first split among the species attributed to the genus *Tritia* separated the Northwest Atlantic species *T. obsoleta* from the East Atlantic/Mediterranean species. This node is inconsistent with the results reported for the nassariid phylogeny (Galindo et al., 2016), in which *T. obsoleta* emerged in an internal position within *Tritia*, although with low bootstrap support. In the past, *T. obsoleta* was assigned as the type species to genus *Ilyanassa* (Stimpson, 1865), which was a taxon that included nassariids from North America (Cernohorsky, 1984). Although *Ilyanassa* had been widely used in previous literature, the internal position of *T. obsoleta* within *Tritia* in Galindo et al. (2016), led these authors to synonymize *Ilyanassa* with *Tritia*. In contrast, our results reveal a correlation between the phylogenetic position of *T. obsoleta* and its geographical distribution, which together with a significant level of genetic divergence (13.7%) support the reinstatement of the genus *Ilyanassa*. To further resolve this part of the tree, it would be also necessary to include *I. trivittata* and other Northwest Atlantic nassariids (Rosenberg, 2009) into the phylogeny, as well as *T. buchardi* from southern Australia and New Zealand, which is close to *Ilyanassa* according to the phylogeny of Galindo et al. (2016).

4.2. Taxonomy of *Tritia*

Within the mostly East Atlantic/Mediterranean group, Clade I comprised 10 species, which are characterized by the presence of a shell with a more or less marked sculpture. The first diverging lineage of Clade I included *T. ephamilla* and *T. elata* + *T. ovoidea*. The former species is endemic to New Zealand and southern Australia whereas the latter two are found in the Mediterranean Sea and

along the West African coasts down to Angola. The inclusion of *T. ephamilla* within *Tritia* was also recovered by Galindo et al (2016), although its exact sister group was not resolved. In addition to the geographic disparity, there is also a prominent morphological difference between *T. ephamilla* (globose with nodulose shell sculpture) and *T. elata* and *T. ovoidea* (slender-ovoid with slight spiral striations). The presence of *T. ephamilla* in this part of the tree could reflect a Thetyan origin of the Northeast Atlantic/Mediterranean mud snails and a subsequent southwards expansion towards tropical waters in the West Africa coasts (Galindo et al., 2016). A striking example of a similar disjoint distribution is constituted by the seagrass genus *Posidonia*, which displays the same contrasting biogeographic pattern. One species, *P. oceanica*, is distributed in the Mediterranean Sea whereas the other species of the genus are restricted to subtropical and temperate Australian waters (Aires et al., 2011). Other Northeast Atlantic/Mediterranean gastropods with a similar disjoint distribution and suspected of having Thetyan origin are the top shell snails of the subfamily Cantharidinae (Uribe et al., 2017b). In this case, the endemics to Oceania were recovered as sister to all Atlantic/ Mediterranean taxa. *Tritia elata* is a circalittoral species typical of soft bottoms of the continental shelf from the southern Iberian Peninsula to Angola. It shows a quite variable shell sculpture along the West African coast where it has been sometimes recorded as *Nassarius semistriatus*, a very similar fossil species extinct during the Pleistocene (Adam & Knudsen, 1984). This last species, as well as the fossil species *Nassarius martinelli* (described by Gili, 1992 from the West Mediterranean Pliocene and differing from *T. elata* by its paucispiral protoconch) likely belong to the stem group of *Tritia*.

The other lineage within Clade I included *T. denticulata* sister to a rather diversified clade including *T. tingitana* sister to the "*T. cuvierii* complex" plus *T. reticulata* and *T. nitida*. The relative position of *T. denticulata* within clade I is in agreement with the Nassariidae molecular phylogeny (Galindo et al., 2016) but here showing high statistical support. *Tritia denticulata* is another circalittoral species distributed in the Alboran Sea and along the West African coasts down to Angola, including the Canary, Madeira and Cabo Verde islands (Rolán & Hernández, 2005). This species is morphologically similar to a group of West African species, namely *N. turbineus*, *N. webbei*, *N. desmoulioides*, and *N. arcadioi* (Rolán & Hernández, 2005), whose ascription to *Tritia* remains to be tested by their incorporation into the molecular phylogeny. In addition, the fossil species *N. clathratus* (Rolán & Hernández, 2005) could belong to the stem lineage of *Tritia*. The

phylogenetic position of *T. tingitana* (endemic of the Strait of Gibraltar), as the second diverging lineage within Clade I, is in clear disagreement with Galindo et al. (2016), who recovered *T. tingitana* as sister to *T. corniculum* with maximal support in a clade equivalent to our Clade III (see below). The two species are morphologically very different, and difficult to misidentify, suggesting a possible mislabeling error.

The last lineage of Clade I included three species corresponding to the "*T. cuvierii* complex" plus *T. reticulata* and *T. nitida* (Galindo et al., 2016; Aissaoui, Galindo, Puillandre, & Bouchet, 2017). Within the "*T. cuvierii* complex", *T. cuvierii* and *T. unifasciata* are sympatric along the Mediterranean coasts, and differ in the size of their shell, protoconch and egg capsules (Moreno & Templado, 1994). *Tritia unifasciata* has faint axial ribs only in the first whorls of the shell. The third species of the complex here studied was *T. tenuicosta*, endemic to the Gulf of Gabès, whose relative position was in agreement to that recovered by Aissaoui, Galindo, Puillandre, & Bouchet (2017). Another two endemic species of the Gulf of Gabès, *T. lanceolata* and *T. djerbaensis* also belong to the "*T. cuvierii* complex", and *T. cuvierii* may also include additional local cryptic species (Aissaoui, Galindo, Puillandre, & Bouchet, 2017). According to Galindo et al. (2016), the West African *T. miga* would be closely related to the "*T. cuvierii* complex". Given its distribution and morphological similarity, the endemic species from Cabo Verde islands, *T. caboverdensis* (Rolán, 1984) may also belong to this complex (pending molecular confirmation).

The closely related and well-known species *T. reticulata* and *T. nitida* have been widely studied from different viewpoints (see Rolán & Luque, 1994; Albaina et al., 2012; Couceiro et al., 2012, and references therein). Both species, sometimes misidentified, share similar life histories and dispersal capacities, but differ in their environmental affinities. The netted dog-whelk *T. reticulata* inhabits a wide range of marine soft bottoms and is mainly an East Atlantic species with a more or less continuous distribution from the British Isles to Morocco and the Canary Islands that enters into western Mediterranean. The estuarine dog-welk *T. nitida* is restricted to sheltered brackish habitats with a patchy distribution in the Mediterranean Sea and Black Sea coasts as well as in the East Atlantic Ocean from Morocco to Norway (Albaina et al., 2012). Therefore, this latter species probably diverged from *T. reticulata* by a habitat shift from marine to brackish waters.

Clade II in our phylogeny (also recovered in Galindo et al., 2016) included *T. varicosa* (often previously recorded as *T. pygmaea*) and *T. incrassata*. Both species are sympatric in the

Mediterranean Sea and along the Northeast Atlantic coast from Sweden to the Iberian Peninsula. They are similar in terms of shell size (about 10 mm) and ornament (little nodules on shell formed by costae and spiral ridges), but the nodules of *T. varicosa* are much smaller, squarer and more upstanding than those of *T. incrassata* (Fretter, Graham & Andrews, 1986). Divergence between both species could have been caused by adaptation to dissimilar habitats: mainly rocky bottoms in *T. incrassata* and soft bottoms with beds of *Zostera* and *Cymodocea* seagrasses in *T. varicosa* (JT, pers. obs.). According to Galindo et al. (2016), *T. senegalensis* and *T. goreensis*, and several other species endemic to Senegal, would be sister to the northern species within this clade.

With a planktotrophic larval stage, *T. incrassata* is widely distributed along the Mediterranean and Northeast Atlantic region. The pairwise uncorrected *p* distance between the two studied individuals of *T. incrassata* from two distant locations (Norway and the Spanish Mediterranean) reached 3.8%, which was even higher than the value obtained for sibling species such as *T. neritea* and *T. pellucida* (Supporting Information Table S4). This result indicates that the diversity of *T. incrassata* was previously underestimated and that it may include putative cryptic species. This hypothesis will need to be further confirmed by the inclusion of data from nuclear genes to discard potential events of incomplete lineage sorting and hybridization (Alexander et al., 2017). A previous phylogeographic study on *T. nitida* suggested the existence of two glacial refugia during the Pleistocene, one in the Atlantic (around the Iberian Peninsula) and the other in the Paleo-Mediterranean Sea (Albaina et al., 2012). It may well be the case that the observed genetic divergence between the two populations of *T. incrassata*-NW and -SP is a result of isolation in the two Pleistocene refugia. After the last glaciation, the Strait of Gibraltar and the Almeria-Oran oceanographic front would have acted as well documented barriers to gene flow between the Atlantic and Mediterranean populations, as reported for *T. nitida* (Albaina et al., 2012) and other marine organisms (Patarnello, Volckaert, & Castilho, 2007). Our results show the need for further studies with dense sampling at the population level along the distribution range of *T. incrassata* in order to determine its diversity and elucidate the evolutionary processes driving its diversification.

Finally, Clade III in the reconstructed tree is composed of eight species with smooth (absence of sculpture) shells as shared derived character. The absence of sculpture may have occurred independently in several lineages of Nassariinae, some of which were already defined in the Early-Middle Miocene (Manganelli, Spadini & Martini, 2010). Phylogenetic relationships within

Clade III are in agreement with those previously reported (Galindo et al., 2016; Aissaoui, Galindo, Puillandre, & Bouchet, 2017), except for the relative phylogenetic position of *T. mutabilis*, which here is moderately supported as sister to *T. pfeifferi* and was not resolved in previous studies. In Galindo et al. (2016), *T. conspersa* was recovered as sister to *T. pfeifferi* within this clade. The earliest divergent lineage within our Clade III includes species of the "*T. corniculum* complex". The pairwise uncorrected *p* distance obtained between *T. pallaryana* (a recently described species from the Gulf of Gabès; Aissaoui, Galindo, Puillandre, & Bouchet, 2017) and *T. corniculum* showed the least value of all comparisons (0.6%; Supporting Information Table S4), and could cast doubts on the taxonomic validity of the former. However, we conservatively maintain *T. pallaryana* as valid given significant ecological and morphological differences (Aissaoui, Galindo, Puillandre, & Bouchet, 2017) as well as because the sequence divergence value falls within the so-called "grey zone" of speciation (Roux et al., 2016). *Tritia elongata*, also endemic of the Gulf of Gabès, was also recovered within the "*T. corniculum* complex", in agreement with Aissaoui, Galindo, Puillandre, & Bouchet (2017). *Tritia corniculum* inhabits sandy-muddy bottoms in shallow, sheltered waters of brackish and marine environments, typically in coastal lagoons (Iannotta, Toscano, & Patti, 2009) with a patchy distribution along the Mediterranean and Northeast Atlantic coasts. Its direct development without a planktonic larval phase, together with the discontinuous distribution of its habitat, may promote genetic isolation among populations and incipient speciation processes, which are reflected in great intra-specific morphological variability (Iannotta, Toscano, & Patti, 2009; Gofas, 2011).

The remaining species of Clade III were *T. mutabilis* (type species of the currently unaccepted genus *Sphaeronassa*) and *T. pfeifferi* sister to a lineage comprising *T. grana* (type species of the currently unaccepted genus *Naytiopsis*) and the flattened-shell sibling species *T. neritea* and *T. pellucida* (previously assigned to the currently unaccepted genus *Cyclope*). While *T. mutabilis* inhabits infralittoral fine sands and muddy sand banks along the Mediterranean coasts, *T. pfeifferi* is an East Atlantic species (from northeastern Spain to Mauritania) adapted to shallow and intertidal sheltered soft bottoms that is replaced by *T. conspersa* in Canary Islands (Gofas, 2011). On the other hand, while *T. grana* inhabits clean, mobile, fine infralittoral sands in open waters, *T. neritea* and *T. pellucida* are characteristic of sandy-muddy shallow bottoms in estuaries, sheltered bays and marine lagoons, often subject to variable salinity (even brackish) waters (Gili & Martinell, 2000;

545 Gofas, 2011).
546
547 **4.3. Protoconch evolution**
548 The robust phylogeny of *Tritia* prompts some considerations about the evolution of the mode of
549 larval development within the genus. Since Thorson (1950), a large body of studies has focused on
550 the evolution of the mode of larval development in marine invertebrates. Transitions between modes
551 of development are considered highly asymmetrical from species with feeding larval stages
552 (planktotrophic) to species with non-feeding larval development (lecithotrophic), with the
553 evolutionary reversal of this transition considered very rare or impossible (Strathmann, 1978;
554 Modica et al., 2020). In both extant and fossil gastropods, the presence of a paucispiral or a
555 multispiral protoconch is used as proxy for the lecithotrophic and planktotrophic alternative modes
556 of development, respectively (Shuto, 1974; Jablonski & Lutz, 1980). The shift in mode of larval
557 development has important evolutionary consequences, as planktotrophic larvae are able to survive
558 longer in the water column and thus have higher dispersal capabilities than lecithotrophic larvae,
559 which barely move from the places where eggs were laid (Shank, 2009). Hence, species with
560 planktotrophic larvae usually are widely distributed and maintain high levels of gene flow between
561 populations, whereas species with lecithotrophic larvae show narrower distribution ranges and are
562 prone to allopatric speciation processes (Collin, 2001; Cunha et al., 2005; Abalde et al. 2017;
563 Modica, 2020).
564 The ancestor of the genus *Tritia* was inferred to have had planktotrophic veliger larvae, as is
565 widely assumed for caenogastropods (Ponder & Lindberg, 1997, 2019; Modica et al., 2020). The
566 lecithotrophic state is a derived condition, which evolved independently in at least three terminal
567 lineages: species within Clade III as well as species of the "*T. cuvierii* complex", and *T. tingitana*
568 within Clade I. In addition, some but not all of the species of the "*T. denticulata* complex" have
569 planktotrophic development, and the potentially closely related *Nassarius turbineus* from the Gulf
570 of Guinea (not included in our phylogeny) exhibits paucispiral protoconch indicative of another
571 independent shift to lecithotrophy within Clade I. The loss of planktotrophy has occurred several
572 other times independently within Nassariinae including some *Reticunassa* species (Galindo et al.,
573 2016). Transitions from planktotrophic to lecithotrophic larval development have been recurrent in
574 diverse caenogastropod lineages (e.g. Lieberman, Allmon, & Eldredge, 1993; Reid, Rumbak, &

575 Thomas, 1996; Duda & Palumbi, 1999; Collin, 2004) and the fossil record from the Northeast
576 Atlantic and Mediterranean shows this trend towards the loss of planktotrophy in several taxa as
577 recently as the Pliocene and Pleistocene periods (Oliverio, 1996). During this evolutionary
578 transition, intermediate forms of development (facultative feeding larvae, short-lived planktotrophs,
579 species with dispersal polymorphisms, and species showing poecilogony, i.e., the presence of the
580 two types of development) should appear (Collin, 2012). However, these intermediate stages are
581 generally ephemeral in evolutionary terms, and either go extinct or evolve into direct developers. In
582 rare cases, the phenotypically plastic intermediates might persist if they show a selective advantage
583 under heterogeneous environmental conditions compared to the two extremes (Collin, 2012). In
584 gastropods, the known cases of poecilogony are prevalent among sea slugs in the suborder
585 Sacoglossa, short-lived planktotrophs are found among calyptraeids, and facultative lecithotrophy
586 has been reported in the nudibranch genus *Phestilla* (Collin, 2012).
587 The frequent and asymmetric transition to lecithotrophy may have key macroevolutionary
588 consequences because it implies shifts in rates of speciation and extinction. On the one hand,
589 species with lecithotrophic development have higher rates of speciation, and thus they are assumed
590 to progressively increase through time compared to widely dispersing species. For instance,
591 Harzhauser & Kowalke (2004) studied the nassariid gastropods from the Neogene Paratethys and
592 observed a trend in the fossil record towards the local appearance of species showing paucispiral
593 protoconch in rather short time periods. On the other hand, regional environmental perturbations
594 could cause the extinction of narrowly ranging species, whereas more broadly dispersed species
595 could survive elsewhere (e.g., Jablonski, 1986). Therefore, higher extinction rates would lower the
596 net diversity of lecithotrophs despite the fact that this condition originates frequently, and this
597 evolutionary pattern could explain the long-term maintenance of planktotrophy (Collin & Moran,
598 2018; Modica et al., 2020). In this regard, several authors have highlighted that planktotrophic
599 species are more resistant to extinction and persist longer on geological time scales relative to
600 lecithotrophic species (e.g. Hansen, 1980; Jablonski, 1986; Crampton et al., 2010). For instance,
601 planktotrophic species of the family Nassariidae from the Neogene fossil deposits of the
602 Atlantic/Mediterranean area had a mean duration of 9.8 million years, whereas the average duration
603 of several non-planktotrophic species was 2.8 million years (Gili & Martinell, 1994).
604 Given the high frequency of the transition to lecithotrophy (together with its enhancing effects

on extinction rates), it is likely that even if most living species of a taxon are included in a molecular phylogeny, the total number of independent transitions to direct development will be underestimated due to ignorance of what may have occurred in extinct lineages (Collin & Moran, 2018). Hence, fossil data appears necessary to testify and supplement the results of molecular data to improve the knowledge of the evolution of this important trait in the life cycle in the East Atlantic and Mediterranean nassariid gastropods (Lozouet & Galindo, 2015; Van Dingenen, Ceuleman, Landau, & da Silva, 2015). For instance, the West Mediterranean Pliocene species *Nassarius martinelli* is distinguished from the extant planktotrophic *T. elata* by its paucispiral protoconch, indicative of lecithotrophic development (Gili, 1992). *Nassarius martinelli* was apparently quite local in South France, inhabiting circallittoral bottoms, and became extinct at the end of the Pliocene or during the first glacial period of the Pleistocene, probably as a consequence of glacio-eustatic processes producing a sharp drop in sea level (Gili, 1992). *Tritia neritea* and *T. pellucida* are the only extant species among Nassariinae gastropods with a depressed, discoidal shell, dorsally convex and flatter in the ventral side. The early Pliocene fossil *Tritia migliorinii* (as *Cyclope migliorinii*) shows the above-mentioned peculiar shell morphology (Gili & Martinell, 1999, 2000) and is considered a member of the stem group. It has a multispiral protoconch (i.e, planktotrophic larval development) implying a putative independent transition to direct development within this lineage of Clade III. Another instance of shift in mode of larval development could be that of some fossil forms closely related to *T. mutabilis* from the Mediterranean and Atlantic Pliocene that may have had a rather short planktotrophic phase (Gili & Martinell, 1990) suggesting yet another transition from plankotrophy to lecithotrophy within Clade III.

4.4. Tempo of diversification

Our reconstructed time tree dates the origin of Nassarinae genera throughout the Oligocene, which is consistent with the fossil record (Lozouet & Galindo, 2015). A trend towards cooler conditions during the Oligocene (Zachos et al., 2001) is likely to have favored temperate taxa (Uribe et al, 2017b). During this period, the onset of deep-water circulation between the Arctic and North Atlantic Oceans (Davies et al., 2001) may have constituted a strong barrier to marine taxa dispersal between North America and Eurasia. In this regard, the separation of *Ilyanassa* from *Tritia* at both

635 sides of the Atlantic and the subsequent diversification of the main eastern lineages occurred right
636 after the Oligocene-Miocene transition. The late Oligocene is thought to have been a time of
637 relatively warm global temperatures while in the early Miocene there was a rapid expansion of the
638 Antarctica ice sheet and large-scale climate fluctuations attributed to an Earth orbital anomaly
639 (Zachos et al., 2001). These global climate oscillations might have triggered diversification events
640 leading to the extant genera within Nassariinae. In parallel, continental drift produced the collision
641 of Laurasia and Gondwana about 19 Mya and the final closure of the Eastern Tethys Seaway (the
642 so-called Terminal Tethyan event) around 14 Mya (Harzhauser et al., 2007; Okay, Zattin, &
643 Cavazza, 2010; Hou & Li, 2018). The closure definitively ended the previous flow of tropical
644 marine gastropods between the Indian Ocean and the proto-Mediterranean Basin (Hamon et al.,
645 2013). In fact, fragmentation of the Tethys Ocean has been suggested as the main driver of the
646 disjunct, endemic and relict distributions of many Tethyan lineages (i.e. Ozawa et al., 2009;
647 Rodríguez-Flores et al., 2020). Accordingly, the puzzling phylogenetic position of the Australian
648 and New Zealand endemic *T. ephamilla*, which diverged about 16 Mya from East Atlantic/
649 Mediterranean taxa (as well as the sister relationship of the Australian *T. buchardi* and the
650 Northwest Atlantic *I. obsoleta*; Galindo et al. 2016), would represent one of the latest split events
651 prior to the closure.
652 The origin of extant species started at the end of the Miocene, when there was a sustained
653 global cooling event that started about 12 Mya and culminated about 5.4 Mya (Herbert et al., 2016),
654 causing an eustatic sea level drop of -10 to -30 m (Hodell et al., 2001). Simultaneously, and because
655 of tectonic movements, the connection between the East Atlantic Ocean and the Mediterranean Sea
656 at the Strait of Gibraltar was closed, resulting in the desiccation of the Mediterranean basin, the
657 well-known Messinian Salinity Crisis (MSC, 5.96 to 5.33 Mya; Krijgsman et al., 1999). Altogether,
658 these climatic, eustatic, and tectonic changes resulted in drastic shifts in the paleoecosystems of the
659 East Atlantic/Mediterranean region that likely triggered speciation, as has been shown for other
660 groups (Davis et al., 2016, Abalde et al., 2017; Uribe et al., 2017b). The ecological adaptation to the
661 variable salinity waters of this period likely promoted the divergence between *T. nitida* and *T.*
662 *reticulata*, between *T. mutabilis* and *T. pfeifferi*, and between *T. grana* and *T. neritea*/ *T. pellucida*,
663 which were dated in the Miocene according to the chronogram. The independent transitions to the
664 direct mode of larval development were also dated in this period. The transition from the Pliocene

665 to the Pleistocene was characterized by a sudden cooling (about 2.6 Mya) and subsequent
666 glacial-interglacial periods with extreme climate oscillations and drastic eustatic sea level changes
667 (Filippelli & Flores, 2009), which may explain the divergence between sibling taxa such as *T.*
668 *pallaryana* and *T. corniculum*, *T. neritea* and *T. pellucida*, and the two distant populations of *T.*
669 *incrassata*.

670 Our estimates of major divergence events within Nassariinae are about 11-24 Mya younger
671 than those previously reported in Galindo et al. (2016), which dated the origin of the lineage leading
672 to *Tritia* and *Ilyanassa* to 48 Mya (Eocene), separation of both genera at 32 Mya (Oligocene), and
673 the diversification of main lineages within *Tritia* during the Miocene. The main difference between
674 the two inferences relies on the calibration points, which in Galindo et al. (2016) were chosen to
675 date the much older Nassariidae origin within Buccinoidea (note that two calibration points were
676 the same in both studies) and the fewer representatives of *Tritia* in their chronogram. Given that our
677 calibration points were chosen to fit better in time the question at hand, and that there is congruence
678 of our estimated dates with climatic, eustatic, and tectonic changes, as well as the rich fossil record
679 of East Atlantic/Mediterranean Nassariinae during the Miocene and Pliocene (Cernohorsky, 1984),
680 we propose the present time tree as our preferred working hypothesis for the timing of the origin
681 and diversification of genus *Tritia*.

682

683 **5. CONCLUSIONS**

684 The reconstructed mitogenomic tree provided high resolution of *Tritia* phylogenetic relationships,
685 and allowed determining that *Gen. inc. sed. vaucheri* does not belong to the genus. Given its
686 distribution, this result calls for a morphological and ecological revision of the West African genus
687 *Naytia*. The strongly supported sister group relationship between the Northwest Atlantic *I. obsoleta*
688 and the three East Atlantic/Mediterranean clades (I-III), justify the reinstatement of the genus
689 *Ilyanassa*, and shows the need for a careful revision of the two genera. Within *Tritia*, the additional
690 described species endemic to West Africa need to be incorporated into the mitogenomic phylogeny.
691 In addition, the notable pairwise divergence between the two *T. incrassata* specimens from Norway
692 and the Spanish Mediterranean strongly suggests the possibility of the existence of cryptic species
693 that needs to be further confirmed with nuclear data and a larger sampling. The robust phylogeny
694 allowed inferring that the ancestor of Nassariinae had planktotrophic larvae and that several

independent transitions to lecithotrophic larvae occurred during the evolutionary history of the group. Hence, it would be interesting to compare morphological and gene expression changes during development of Nassariinae lecithotrophic larvae in search for footprints of convergence. The inferred divergence dates suggest an important role of climatic, eustatic, and tectonic changes during the Oligocene, Miocene, and Pleistocene influencing local Atlantic/Mediterranean paleoecosystems and promoting the origin, main lineage diversification, and recent speciation events within *Tritia*, respectively. Several recent divergences between some pairs of close species could be due to a habitat shift from open marine to sheltered brackish waters. Our study indicates that mt genomes could render similar robust results when applied to other Nassariinae genera and would be highly useful in reconstructing a robust phylogeny of the entire Nassariidae family, hence providing the long-needed framework to understand diversification and adaptation processes underpinning the evolutionary success of this family.

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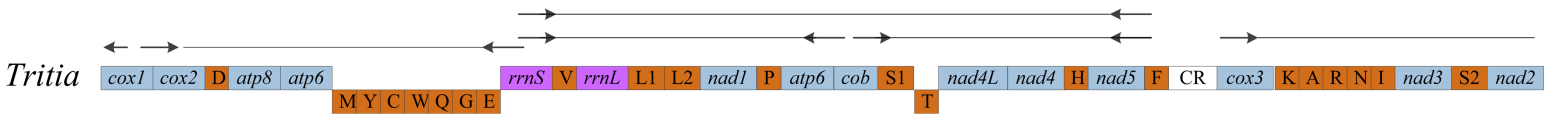
Figure captions

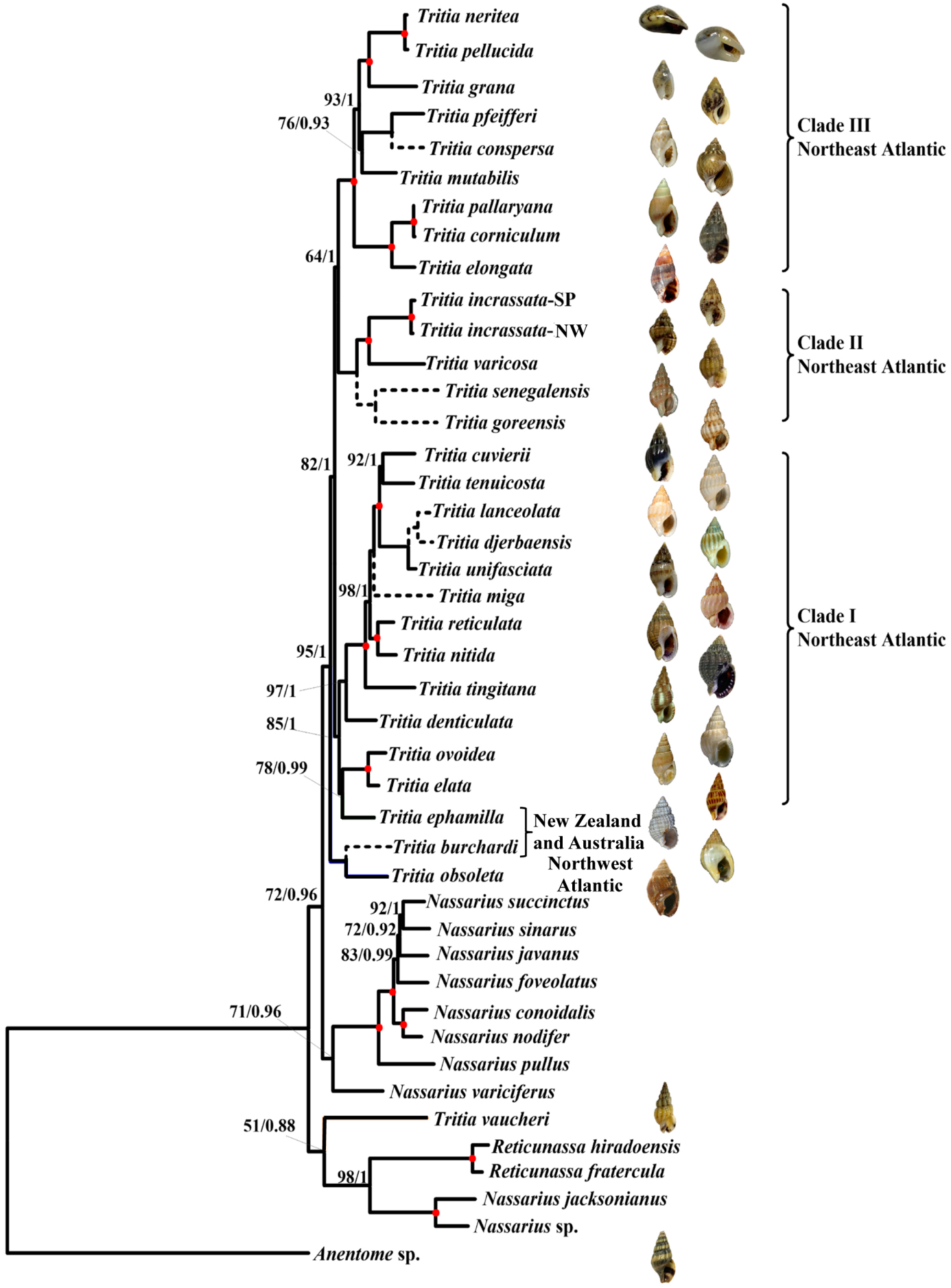
Figure 1. Gene order of *Tritia* mitogenomes. All newly sequenced mt genomes shared identical genome organization. The genes encoded in the major and minor strands are shown in the top and bottom rows, respectively. Genes encoding for proteins (blue), rRNAs (pink), and tRNAs (red) are depicted with different colors. The relative positions of the primers for long PCR are shown.

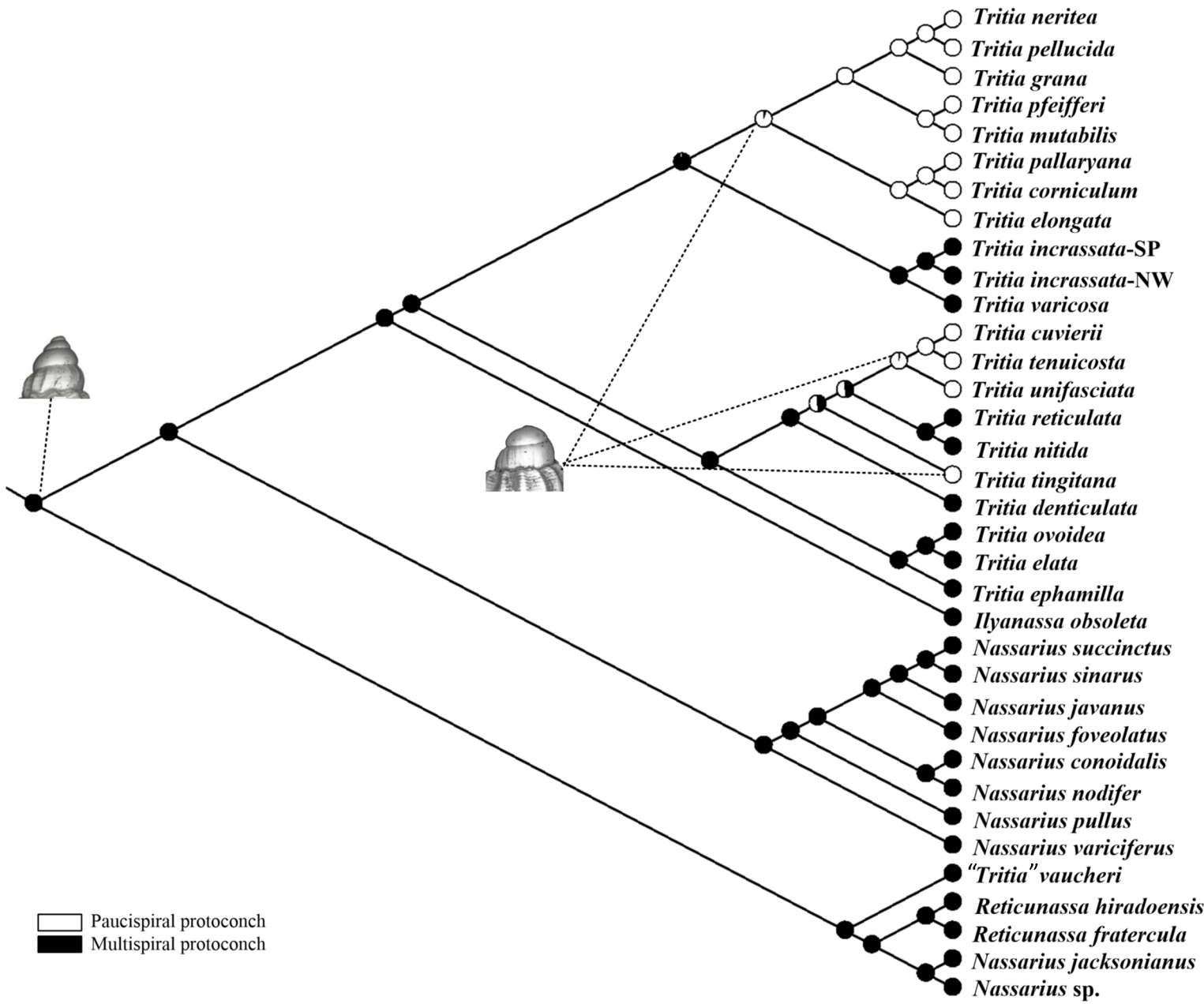
Figure 2. Phylogenetic relationships within Nassariinae based on the nucleotide sequences of 13 protein-coding genes plus two rRNA genes. The Bayesian inference (BI) phylogram is shown. The non-nassariinae *Anentome* sp. was used as outgroup. The three Northeast clades are indicated. Numbers at nodes are statistical support values for ML (bootstrap proportions in percentage)/BI (posterior probabilities). Solid red circles represent nodes with maximum support values. The bar indicates substitutions per site. Additional *Tritia* species whose relative phylogenetic positions were resolved in Galindo et al. (2016) but were not included in this study are shown with a dashed line. Ventral images of the voucher specimens are shown.

Figure 3. Ancestral character state reconstruction of *Tritia* protoconch (paucispiral *versus* multispiral) using the ML model Mk1 in Mesquite. Pie charts represent the statistical support at every node.

Figure 4. Chronogram with age estimates of major divergence events within Nassariinae based on the nucleotide sequences of the concatenated mitochondrial protein coding genes, and using Bayesian relaxed dating methods (BEAST). Horizontal bars represent 95% credible intervals of relevant nodes, and calibration constraints are indicated with an asterisk on the corresponding nodes. Dates (and highest posterior density intervals, HPD) are in millions of years. Geological epochs are indicated.


Tritia
cox1
cox2
D
atp8
atp6
M
Y
C
W
Q
G
E
rrnS
V
rrnL
L1
L2
nad1
P
atp6
cob
S1
T
nad4L
nad4
H
nad5
F
CR
cox3
K
A
R
N
I
nad3
S2
nad2


Tritia neritea
Tritia pellucida
Tritia grana
93/1
76/0.93
Tritia pfeifferi
Tritia conspersa
Tritia mutabilis
Tritia pallaryana
Tritia corniculum
64/1
Tritia elongata
Tritia incrassata-SP
Tritia incrassata-NW
Tritia varicosa
Tritia senegalensis
Tritia goreensis
82/1
92/1
Tritia cuvierii
Tritia tenuicosta
Tritia lanceolata
Tritia djerbaensis
Tritia unifasciata
98/1
Tritia miga
Tritia reticulata
95/1
Tritia nitida
97/1
Tritia tingitana
85/1
Tritia denticulata
Tritia ovoidea
78/0.99
Tritia elata
Tritia ephamilla
Tritia burchardi
Tritia obsoleta
72/0.96
92/1
Nassarius succinctus
72/0.92
Nassarius sinarus
83/0.99
Nassarius javanus
Nassarius foveolatus
71/0.96
Nassarius conoidalis
Nassarius nodifer
Nassarius pullus
Nassarius variciferus
Tritia vaucheri
51/0.88
Reticunassa hiradoensis
Reticunassa fratercula
98/1
Nassarius jacksonianus
Nassarius sp.
Anentome sp.
1
Clade III
Northeast Atlantic
Clade II
Northeast Atlantic
Clade I
Northeast Atlantic
New Zealand
and Australia
Northwest
Atlantic


Tritia neritea
Tritia pellucida
Tritia grana
Tritia pfeifferi
Tritia mutabilis
Tritia pallaryana
Tritia corniculum
Tritia elongata
Tritia incrassata-SP
Tritia incrassata-NW
Tritia varicosa
Tritia cuvierii
Tritia tenuicosta
Tritia unifasciata
Tritia reticulata
Tritia nitida
Tritia tingitana
Tritia denticulata
Tritia ovoidea
Tritia elata
Tritia ephamilla
Ilyanassa obsoleta
Nassarius succinctus
Nassarius sinarus
Nassarius javanus
Nassarius foveolatus
Nassarius conoidalis
Nassarius nodifer
Nassarius pullus
Nassarius variciferus
"Tritia" vaucheri
Reticunassa hiradoensis
Reticunassa fratercula
Nassarius jacksonianus
Nassarius sp.
Paucispiral protoconch
Multispiral protoconch

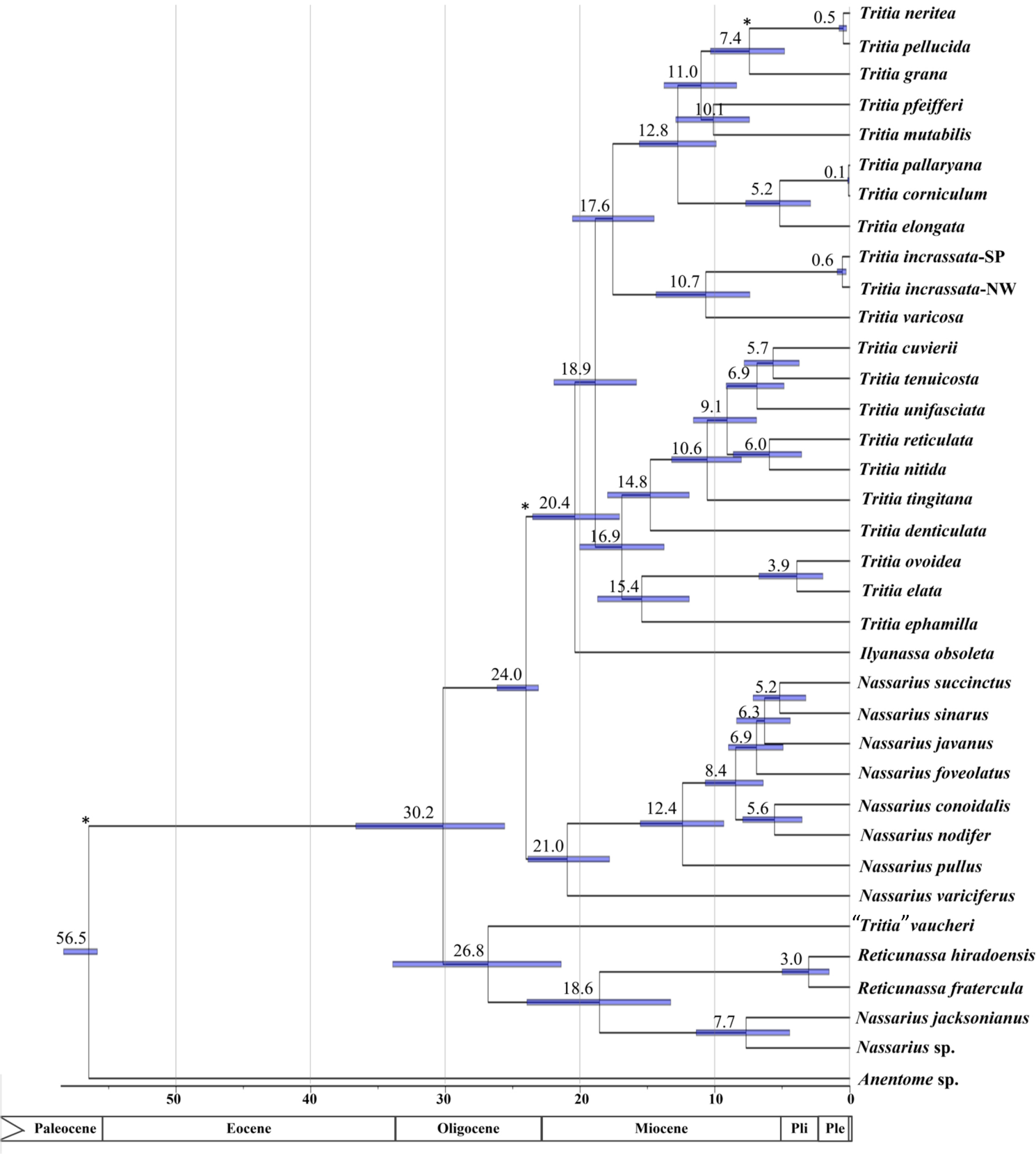

Tritia neritea
Tritia pellucida
Tritia grana
Tritia pfeifferi
Tritia mutabilis
Tritia pallaryana
Tritia corniculum
Tritia elongata
Tritia incrassata-SP
Tritia incrassata-NW
Tritia varicosa
Tritia cuvierii
Tritia tenuicosta
Tritia unifasciata
Tritia reticulata
Tritia nitida
Tritia tingitana
Tritia denticulata
Tritia ovoidea
Tritia elata
Tritia ephamilla
Ilyanassa obsoleta
Nassarius succinctus
Nassarius sinarus
Nassarius javanus
Nassarius foveolatus
Nassarius conoidalis
Nassarius nodifer
Nassarius pullus
Nassarius variciferus
"Tritia" vaucheri
Reticunassa hiradoensis
Reticunassa fratercula
Nassarius jacksonianus
Nassarius sp.
Anentome sp.
0.5
7.4
11.0
10.1
12.8
0.1
5.2
17.6
0.6
10.7
5.7
18.9
6.9
9.1
10.6
6.0
14.8
20.4
16.9
3.9
15.4
24.0
5.2
6.3
6.9
8.4
30.2
12.4
5.6
21.0
56.5
26.8
3.0
18.6
7.7
50
40
30
20
10
0
Paleocene
Eocene
Oligocene
Miocene
Pli
Ple

Table 1. Mitochondrial (mt) genomes analyzed in this study.

New mt genomes

Species	Location	Collector	No. reads	Coverage (x)	Length (bp)	Genbank Acc. No.	Voucher
Tritia corniculum	Ilha da Armona, Portugal	CLMA	34 502	75	15 114	MT755650	MNCN:ADN: 118970
Tritia cuvierii	Cabo de Palos, Spain	JT	36 582	306	15 185	MT755651	MNCN:ADN: 118971
Tritia grana	Cabo de Palos, Spain	JT	40 296	131	15 198	MT762151	MNCN:ADN: 118972
Tritia incrassata -SP	Cabo de Palos, Spain	JT	30 800	53	15 159	MT762153	MNCN:ADN: 118973
Tritia incrassata -NW	Bergen, Norway	David Osca	38 716	151	15 170	MT762152	MNCN:ADN: 118974
Tritia mutabilis	Market, Madrid, Spain	YY	40 182	250	15 148	MT762154	MNCN:ADN: 118975
Tritia neritea	Vigo, Spain	SA	35 082	216	15 179	MT762155	MNCN:ADN: 118976
Tritia pellucida	Mar Menor, Spain	JT	40 234	317	15 175	MT768039	MNCN:ADN: 118977
Tritia pfeifferi	Praia dos Cavacos, Portugal	CLMA	43 804	76	15 142	MT768040	MNCN:ADN: 118978
Tritia unifasciata	Mar Menor, Spain	JT	43 288	322	15 168	MT768043	MNCN:ADN: 118979
Tritia vaucheri	Isla Canela, Spain	CLMA	58 170	83	15 153	MT768044	MNCN:ADN: 118980
Tritia denticulata	Candelaria, Spain	—	2 142 656	19 059	15 167	MT755652	MNHN-IM-2009-21546
Tritia ephamilla	Kermadec Ridge, New Zealand	—	1 849 562	14 802	15 157	MT755654	MNHN-IM-2009-24014
Tritia pallaryana	Golfe de Gabès, Tunisie	Chrifa Aissaoui	2 515 502	21 974	15 144	MT762157	MNHN-IM-2009-30939
Tritia tenuicosta	Golfe de Gabès, Tunisie	Chrifa Aissaoui	2 494 246	19 378	15 169	MT768042	MNHN-IM-2013-31865
Tritia elongata	Errimel, Tunisie	Chrifa Aissaoui	2 133 232	18 698	15 145	MT755653	MNHN-IM-2013-32570
Tritia nitida	Vigo, Spain	Samuel Abalde	2 415 740	21 498	15 157	MT762156	MNCN:ADN: 118981
Tritia varicosa	Ponta da Piedade, Portugal	CLMA	2 765 768	23 350	15 142	MT768041	MNCN:ADN: 118982
Tritie elata	Ponta da Piedade, Portugal	CLMA	2 493 798	21 897	15 167	MT768045	MNCN:ADN: 118983
Tritia tingitana	Isla de Tarifa, Spain	Serge Gofas	—	—	13 337	MW194096	MNCN:ADN: 118984
Tritia ovoidea	Cañón de Carchuna, Spain	Serge Gofas	—	—	14 889	MW194095	MNCN:ADN: 118985
Anentome sp.	Aquarium market, Madrid, Spain	YY	2 528 802	19 514	15 069	MT755649	MNCN:ADN: 118986

Genbank mt genomes

Species	Length (bp)	Accession No.	Reference
Tritia obsoleta	15 263	DQ238598	Simison, Lindberg, & Boore, 2006
Tritia reticulata	15 271	EU827201	Cunha, Grande, & Zardoya, 2009
Nassarius variciferus	15 269	KM603509	Yang, Li, Kong, & Yu, 2018
Nassarius succinctus	15 329	KT768016	Yang, Li, Kong, & Yu, 2019
Nassarius nodifer	15 337	KT818617	Yang, Li, Kong, & Yu, 2019
Nassarius conoidalis	15 332	KT826694	Yang, Li, Kong, & Yu, 2019
Nassarius pullus	15 278	KT900947	Yang, Li, Kong, & Yu, 2019
Nassarius sinarus	15 325	MH346208	Yang, Li, Kong, & Yu, 2019
Nassarius foveolatus	15 343	MH346209	Yang, Li, Kong, & Yu, 2019
Nassarius javanus	15 325	MH346210	Yang, Li, Kong, & Yu, 2019
Reticunassa fratercula	15 174	KT826695	Yang, Li, Kong, & Yu, 2018
Reticunassa hiradoensis	15 194	MG744569	Yang, Li, Kong, & Yu, 2018
Nassarius jacksonianus	15 234	MH346212	Yang, Li, Kong, & Yu, 2019
Nassarius sp.	15 240	MH346211	Yang, Li, Kong, & Yu, 2019

Table S1. Standard and Long PCR primers for *Tritia* mitogenomes.

Tritia corniculum	Sequenced by Allgenetics, with a buccinoid species in the same library	
Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
COI-tritiaF	ACWGCYCAYGCTTTYGTAATAAT	*cox1* (400)
COI-tritiaR	TGYATNCCTCGTCATCGYATRTT	

Tritia cuvierii	Sequenced by Allgenetics, in a whole library	
Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
LCO1490 F	GGTCAACAAATCATAAAGATATTGG	*cox1* (709)
HCO2198 R	TTAACTTCAGGGTGACCAAAAAATCA	

Tritia grana	Sequenced by Allgenetics, with a cone species in the same library	
Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	

cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
LCO1490 F	GGTCAACAAATCATAAAGATATTGG	*cox1* (709)
HCO2198 R	TTAACTTCAGGGTGACCAAAAAATCA	

Tritia incrassata-sp Sequenced by Allgenetics, with a cone species in the same library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
COINassaF	TCTACAAATCATAAAGACATTGG	*cox1* (700)
COINassaR	ACYTCAGGATGACCAAARAATCA	

Tritia incrassata-nw Sequenced by Allgenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
COINassaF	TCTACAAATCATAAAGACATTGG	*cox1* (700)
COINassaR	ACYTCAGGATGACCAAARAATCA	

Tritia mutabilis Sequenced by Allgenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	

12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
COINassaF	TCTACAAATCATAAAGACATTGG	*cox1* (700)
COINassaR	ACYTCAGGATGACCAAARAATCA	

Tritia neritea	Sequenced by Allgenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
LCO1490 F	GGTCAACAAATCATAAAGATATTGG	*cox1* (709)
HCO2198 R	TTAACTTCAGGGTGACCAAAAAATCA	

Tritia pellucida	Sequenced by Allgenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
LCO1490 F	GGTCAACAAATCATAAAGATATTGG	*cox1* (709)
HCO2198 R	TTAACTTCAGGGTGACCAAAAAATCA	

Tritia pfeifferi	Sequenced by Allgenetics, with a buccinoid species in the same library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
COINassaF	TCTACAAATCATAAAGACATTGG	*cox1* (700)
COINassaR	ACYTCAGGATGACCAAARAATCA	

Tritia unifascita	Sequenced by Allgenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
LCO1490 F	GGTCAACAAATCATAAAGATATTGG	*cox1* (709)
HCO2198 R	TTAACTTCAGGGTGACCAAAAAATCA	

Tritia vaucheri	Sequenced by Allgenetics, with a buccinoid species in the same library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)

COINassaF	TCTACAAATCATAAAGACATTGG	*cox1* (700)
COINassaR	ACYTCAGGATGACCAAARAATCA	

Tritia denticulata Sequenced by NIMGenetics, in a whole library

Long PCR

Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
coblaF	GAYCCWGARAAYTTTATYCCTGCTAAYCC	*cob-trnF* (4.0K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	

cox1 Genbank Acc. No: KY451292

Primer Link *cytb*

Primer	Sequence 5'-3'	Fragment (bp)
cytbF	GGWTAYGTWYTWCCWTGRGGWCARAT	*cytb* (0.5K)
cytbR	GCRTAWGCRAAWARRAARTAYCAYTCWGG	

Tritia ephamilla Sequenced by NIMGenetics, in a whole library

Long PCR

Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.4K)
coblaR	GCYCCTCARAARGATATYTGACCTCARGG	
coblaF	GAYCCWGARAAYTTTATYCCTGCTAAYCC	*cob-trnF* (4.0K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	

cox1 Genbank Acc. No: KY451298

Primer Link *cytb*

Primer	Sequence 5'-3'	Fragment (bp)
cytbF	GGWTAYGTWYTWCCWTGRGGWCARAT	*cytb* (0.5K)
cytbR	GCRTAWGCRAAWARRAARTAYCAYTCWGG	

Tritia pallaryana Sequenced by NIMGenetics, in a whole library

Long PCR

Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)

cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
COI-tritiaF	ACWGCYCAYGCTTTYGTAATAAT	*cox1* (400)
COI-tritiaR	TGYATNCCTCGTCATCGYATRTT	

Tritia tenuicosta Sequenced by NIMGenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.4K)
coblaR	GCYCCTCARAARGATATYTGACCTCARGG	
coblaF	GAYCCWGARAAYTTTATYCCTGCTAAYCC	*cob-trnF* (4.0K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
cox1 Genbank Acc. No: KY489424		
Primer Link *cytb*		
Primer	Sequence 5'-3'	Fragment (bp)
cytbF	GGWTAYGTWYTWCCWTGRGGWCARAT	*cytb* (0.5K)
cytbR	GCRTAWGCRAAWARRAARTAYCAYTCWGG	

Tritia elongata Sequenced by NIMGenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
cox1 Genbank Acc. No: KY489440		

Tritia nitida Sequenced by NIMGenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)

12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
LCO1490 F	GGTCAACAAATCATAAAGATATTGG	*cox1* (709)
HCO2198 R	TTAACTTCAGGGTGACCAAAAAATCA	

Tritia varicosa Sequenced by NIMGenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
16slaF	GTGCAAAGGTAGCATAATCATTTGCCT	*rrnL-trnF* (6.1K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
COINassaF	TCTACAAATCATAAAGACATTGG	*cox1* (700)
COINassaR	ACYTCAGGATGACCAAARAATCA	

Tritia elata Sequenced by NIMGenetics, in a whole library

Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
16slaF	GTGCAAAGGTAGCATAATCATTTGCCT	*rrnL-trnF* (6.1K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		
Primer	Sequence 5'-3'	Fragment (bp)
COINassaF	TCTACAAATCATAAAGACATTGG	*cox1* (700)
COINassaR	ACYTCAGGATGACCAAARAATCA	

Tritia ovoidea	Sequenced by Sanger	
Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (5.7K)
16SlaR	ATGCTGTTATCCCTACGGTAACTAATT	
16SZouF	GCGGTACTCTGACCGTGCAA	*rrnL-cob* (2.5K)
coblaR	GCYCCTCARAARGATATYTGACCTCARGG	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
15F	TCAGCYTGTGGATTTGRARAT	*trnH-trnF* (1.6K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
Walking Primers		
Primer	Sequence 5'-3'	Fragment (bp)
1F	TGATTTCTTARGAGAGGTTCA	*TrnQ-rrnS* (1K)
1R	TGCTATGTTACGACTTATCTC	
2F	AAGCTRTTGGGTTCATACCCC	*TrnM-TrnE* (0.5K)
2R	TAGATTTTCATTCTAAARGRATA	
3F	ATGCTTGTAGACATTTTTTCTTC	*atp6-trnC* (0.9K)
3R	TCGATTTTGCARRTCGATGTT	
4F	TTTTAYGGTCARTGTTCYGAAAT	*cox2-atp6* (0.8K)
4R	ACAATATGYCCRGCYCTTATRTT	
5F	ATGAGCCTATGAGGACAAYTAGGATT	*cox2-trnD* (0.7K)
5R	GYRACRTAAGRCTGACAAYCT	
6F	GAYATTATRCTYCAYGAYACHTAYTA	*cox1-cox2* (0.7K)
6R	TCATAGCTTCARTATCATTGRTG	
7F	AAYATRCGATGACGAGGRATRCA	*cox1* (0.9K)
7R	GCYTCYCABACAATTACYATRAA	
9F	AGGGCTGCTAACTTTGTTTTG	*trnS-cox1* (1.1K)
9R	ACRTTRTAAAGTTGRTCRTCACC	
10F	CTAGCTGTTAATTAGRAGAAT	*trnN-nd2* (0.75K)
10R	ATRAARTAYTTWACRGCYGAYTG	
11F	TTYTTYTGAGCTTAYTTTCAYAG	*cox3-trnI* (0.87K)
11R	ACATCAATGATTYCCGTTCAT	
15F	TCAGCYTGTGGATTTGRARAT	*nd5* (0.9K)
15R	TTRTGRATAAATATHCCDGCRCA	
16F	ATTGGNGCHAAYTAYGAAAAYGA	*nd5-trnF* (0.9K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
Standard PCR		
Primer	Sequence 5'-3'	Fragment (bp)
12F	ATGGCRCGTAATCCTTTTCATTT	*cox3-trnA* (0.8K)
12R	CTRAATGCAAATCARRTCTTT	
13F	TTTGAAGCTTCTTTAATTCCWAC	*nd4-trnH* (0.8K)
13R	ATYTYCAAATCCACARGCTGA	
coblaF	GAYCCWGARAAYTTTATYCCTGCTAAYCC	*cob-nd4* (0.9K)

14R	TTKACYCTATTTTGMCTYGCTAA	
18F	DCATTCTGCCTGTTTAKCAAA	*rrnL-trnL2* (0.8K)
18R	GGGCTTAAACCTAATGCACTT	
19F	AATGCAATTGACTTAGGMTCA	*trnL1-trnP* (1K)
19R	ACCCAAGCTYTAGCTTCCAAT	
20F	TTGGCAGTCGCTTTTTTTACTCT	*nd1-nd6* (1K)
20R	CTAAARAYAATTARYGCTCTCAT	
21F	ATTAGCATTGGAAGCTARAGC	*trnP-cob* (0.6K)
21R	AARATRGGRTGHACTTTTCGAAT	
22F	ATGCGAAGTCCYATTCGAAAAGT	*cob* (1K)
22R	ACMGGACAAGCYCCAATTCAWGT	
LCO1490 F	GGTCAACAAATCATAAAGATATTGG	*cox1* (709)
HCO2198 R	TTAACTTCAGGGTGACCAAAAAATCA	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnL-rrnS* (1.2K)
16sZouR	TCACGTAGAATTTTAATGGTCG	
coblaF	GAYCCWGARAAYTTTATYCCTGCTAAYCC	*cob-nd4* (1.2K)
nd4lnd4R	GGTAATGAAGCTGCTACAGTGTA	

Tritia tingitana	Sequenced by Sanger	
Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
16SZouF	GCGGTACTCTGACCGTGCAA	*rrnL-cob* (2.5K)
coblaR	GCYCCTCARAARGATATYTGACCTCARGG	
12F	ATGGCRCGTAATCCTTTTCATTT	*cox3-cox1* (3K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
5F	ATGAGCCTATGAGGACAAYTAGGATT	*cox2-rrnS* (3K)
12slaR	ATAGGCTGCACCTTGATCTGACGTYTT	
15F	TCAGCYTGTGGATTTGRARAT	*trnH-trnF* (1.6K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
coblaF	GAYCCWGARAAYTTTATYCCTGCTAAYCC	*cob-trnH* (2.5K)
13R	ATYTYCAAATCCACARGCTGA	
Walking Primers		
Primer	Sequence 5'-3'	Fragment (bp)
1F	TGATTTCTTARGAGAGGTTCA	*TrnQ-rrnS* (1K)
1R	TGCTATGTTACGACTTATCTC	
2F	AAGCTRTTGGGTTCATACCCC	*TrnM-TrnE* (0.5K)
2R	TAGATTTTCATTCTAAARGRATA	
3F	ATGCTTGTAGACATTTTTTCTTC	*atp6-trnC* (0.9K)
3R	TCGATTTTGCARRTCGATGTT	
4F	TTTTAYGGTCARTGTTCYGAAAT	*cox2-atp6* (0.8K)
4R	ACAATATGYCCRGCYCTTATRTT	
5F	ATGAGCCTATGAGGACAAYTAGGATT	*cox2-trnD* (0.7K)
5R	GYRACRTAAGRCTGACAAYCT	
9F	AGGGCTGCTAACTTTGTTTTG	*trnS-cox1* (1.1K)

9R	ACRTTRTAAAGTTGRTCRTCACC	
10F	CTAGCTGTTAATTAGRAGAAT	*trnN-nd2* (0.75K)
10R	ATRAARTAYTTWACRGCYGAYTG	
11F	TTYTTYTGAGCTTAYTTTCAYAG	*cox3-trnI* (0.87K)
11R	ACATCAATGATTYCCGTTCAT	
12F	ATGGCRCGTAATCCTTTTCATTT	*cox3-trnA* (0.8K)
12R	CTRAATGCAAATCARRTCTTT	
13F	TTTGAAGCTTCTTTAATTCCWAC	*nd4-trnH* (0.8K)
13R	ATYTYCAAATCCACARGCTGA	
coblaF	GAYCCWGARAAYTTTATYCCTGCTAAYCC	*cob-nd4* (0.9K)
14R	TTKACYCTATTTTGMCTYGCTAA	
15F	TCAGCYTGTGGATTTGRARAT	*nd5* (0.9K)
15R	TTRTGRATAAATATHCCDGCRCA	
16F	ATTGGNGCHAAYTAYGAAAAYGA	*nd5-trnF* (0.9K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
18F	DCATTCTGCCTGTTTAKCAAA	*rrnL-trnL2* (0.8K)
18R	GGGCTTAAACCTAATGCACTT	
19F	AATGCAATTGACTTAGGMTCA	*trnL1-trnP* (1K)
19R	ACCCAAGCTYTAGCTTCCAAT	
20F	TTGGCAGTCGCTTTTTTTACTCT	*nd1-nd6* (1K)
20R	CTAAARAYAATTARYGCTCTCAT	
21F	ATTAGCATTGGAAGCTARAGC	*trnP-cob* (0.6K)
21R	AARATRGGRTGHACTTTTCGAAT	
22F	ATGCGAAGTCCYATTCGAAAAGT	*cob* (1K)
22R	ACMGGACAAGCYCCAATTCAWGT	
Standard PCR		
Primer	Sequence 5'-3'	Fragment (bp)
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnL-rrnS* (1.2K)
16sZouR	TCACGTAGAATTTTAATGGTCG	
cob-12870F	GGGTATGTCTTACCCTGAGGTCAGAT	*cob* (0.4K)
cob-12870R	GCATACGCAAAGAGGAAGTATCATTCTGG	

Anentome sp.	Sequenced by NIMGenetics, in a whole library	
Long PCR		
Primer	Sequence 5'-3'	Fragment (bp)
cox1laF	AAYATRCGATGACGAGGRATRCARTTTGA	*cox1-rrnS* (4K)
12SlaR	ATAGGCTGCACCTTGATCTGACGTYTT	
12SlaF	CAGTTTGTATACCGTCGTCGTCAGGT	*rrnS-cob* (4.5K)
cobla2R	GGRTTAGCWGGRATAAARTTYTCWGGRTC	
cobla2F	CCYTGAGGTCARATATCYTTYTGAGGRGC	*cob-trnF* (4.3K)
trnF-R	CACCCTAGCATCTTCAGTGCTATGCTCT	
cox3la2F	ATGGCRCGNAATCCTTTTCATTTAGTWGARTT	*cox3-cox1* (2.5K)
cox1laR	CGAGGAAAAGCYATRTCAGGAGC	
Primer Link *cox1*		

Primer	Sequence 5'-3'	Fragment (bp)
LCO1490 F	GGTCAACAAATCATAAAGATATTGG	*cox1* (709)
HCO2198 R	TTAACTTCAGGGTGACCAAAAAATCA	

Table S2. Best fit partitions and substitution models.

	Set Partition (Conducted by PartitionFinder 2)	Best Model for BI (Selected by PartitionFinder 2)	Best Model for ML (Selected by IQtree 1.6.10)
Best Partition CDS genes (BIC= 254577.82)	*atp6-8* 1th	TRN+G	TN+F+G4
	atp6-8 2th	K81UF+I	K3Pu+F+I
	atp6-8 3th	TVM+I+G	K3Pu+F+I+G4
	cox1-2-3 1th	TRN+I+G	TN+F+I+G4
	cox1-2-3 2th	TVM+I+G	TVM+F+I+G4
	cox1-2-3 3th	GTR+I+G	TVM+F+I+G4
	cob 1th	TRN+I+G	TIM2+F+I+G4
	cob 2th	TVM+I+G	TVM+F+I+G4
	cob 3th	K81UF+I+G	K3Pu+F+I+G4
	nad1-2-3-4-4L-5-6 1th	GTR+I+G	TIM3+F+I+G4
	nad1-2-3-4-4L-5-6 2th	GTR+I+G	GTR+F+I+G4
	nad1-2-3-4-4L-5-6 3th	GTR+I+G	TVM+F+I+G4
Best Partition to rRNA genes (BIC= 26625.61)	*rrnS-L*	GTR+I+G	GTR+F+I+G4

Table S3. Mitochondrial genome features

Tritia corniculum 15,114 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-747	incomplete	—	TAG	15
tRNA-*Lys*	H	763-827	65			1
tRNA-*Ala*	H	829-896	68			9
tRNA-*Arg*	H	906-974	69			5
tRNA-*Asn*	H	980-1047	68			15
tRNA-*Ile*	H	1063-1130	68			3
Nad3	H	1134-1487	354	ATG	TAA	0
tRNA-*Ser*	H	1488-1555	68			0
Nad2	H	1556-2610	1055	ATG	TA	0
Cox1	H	2611-4146	1536	ATG	TAA	29
Cox2	H	4176-4862	687	ATG	TAA	-2
tRNA-*ASp*	H	4861-4928	68			1
Atp8	H	4930-5088	159	ATG	TAA	7
Atp6	H	5096-5791	696	ATG	TAA	38
tRNA-*Met*	L	5830-5896	67			3
tRNA-*Tyr*	L	5900-5967	68			1
tRNA-*Cys*	L	5969-6033	65			0
tRNA-*Trp*	L	6034-6099	66			1
tRNA-*Gln*	L	6101-6162	62			1
tRNA-*Gly*	L	6164-6231	68			11
tRNA-*Glu*	L	6243-6307	65			0
12s	H	6308-7265	958			0
tRNA-*Val*	H	7266-7333	68			0
16s	H	7334-8685	1352			0
tRNA-*Leu*	H	8686-8757	72			2
tRNA-*Leu*	H	8760-8828	69			0
Nad1	H	8829-9770	942	ATG	TAA	6
tRNA-*Pro*	H	9777-9844	68			1
Nad6	H	9846-10346	501	ATG	TAG	5
Cytb	H	10352-11491	1140	ATG	TAA	9
tRNA-*Ser*	H	11502-11565	64			0
tRNA-*Thr*	L	11566-11630	65			20
Nad4L	H	11651-11947	297	ATG	TAG	11
Nad4	H	11959-13314	1356	ATA	TAG	-1
tRNA-*His*	H	13314-13378	65			0
Nad5	H	13379-15100	1722	ATG	TAG	14
tRNA-*Phe*	H	missing	—			—

Tritia cuvierii 15,185 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-776	incomplete	—	TAA	12
tRNA-*Lys*	H	789-853	65			2
tRNA-*Ala*	H	856-922	67			10
tRNA-*Arg*	H	933-1001	69			8
tRNA-*Asn*	H	1010-1077	68			17
tRNA-*Ile*	H	1095-1162	68			3
Nad3	H	1166-1519	354	ATG	TAG	0
tRNA-*Ser*	H	1520-1587	68			0
Nad2	H	1588-2642	1055	ATG	TA	0
Cox1	H	2643-4178	1536	ATG	TAA	26
Cox2	H	4205-4891	687	ATG	TAA	-2
tRNA-*ASp*	H	4890-4957	68			1
Atp8	H	4959-5117	159	ATG	TAA	6
Atp6	H	5124-5819	696	ATG	TAA	42
tRNA-*Met*	L	5862-5928	67			4
tRNA-*Tyr*	L	5933-5999	67			1
tRNA-*Cys*	L	6001-6066	66			0
tRNA-*Trp*	L	6067-6132	66			0
tRNA-*Gln*	L	6133-6196	64			1
tRNA-*Gly*	L	6198-6264	67			14
tRNA-*Glu*	L	6279-6343	65			0
12s	H	6344-7302	959			0
tRNA-*Val*	H	7303-7370	68			0
16s	H	7371-8723	1353			0
tRNA-*Leu*	H	8724-8792	69			2
tRNA-*Leu*	H	8795-8863	69			0
Nad1	H	8864-9805	942	ATG	TAA	5
tRNA-*Pro*	H	9811-9878	68			1
Nad6	H	9880-10380	501	ATG	TAA	5
Cytb	H	10386-11525	1140	ATG	TAA	9
tRNA-*Ser*	H	11535-11599	65			0
tRNA-*Thr*	L	11600-11667	68			25
Nad4L	H	11693-11989	297	ATG	TAG	11
Nad4	H	12001-13356	1356	ATA	TAG	-1
tRNA-*His*	H	13356-13421	66			1
Nad5	H	13423-15144	1722	ATG	TAG	41
tRNA-*Phe*	H	missing	—			—

Tritia denticulata 15,167 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-771	incomplete	—	TAA	15
tRNA-*Lys*	H	787-852	66			3
tRNA-*Ala*	H	856-923	68			8
tRNA-*Arg*	H	932-1002	71			7
tRNA-*Asn*	H	1010-1076	67			17
tRNA-*Ile*	H	1094-1161	68			3
Nad3	H	1165-1518	354	ATG	TAA	0
tRNA-*Ser*	H	1519-1586	68			0
Nad2	H	1587-2641	1055	ATG	TA	0
Cox1	H	2642-4177	1536	ATG	TAA	22
Cox2	H	4200-4886	687	ATG	TAA	-2
tRNA-*Asp*	H	4885-4952	68			1
Atp8	H	4954-5112	159	ATG	TAA	7
Atp6	H	5120-5815	696	ATG	TAA	42
tRNA-*Met*	L	5858-5924	67			6
tRNA-*Tyr*	L	5931-5998	68			1
tRNA-*Cys*	L	6000-6063	64			0
tRNA-*Trp*	L	6064-6129	66			-3
tRNA-*Gln*	L	6127-6193	67			-1
tRNA-*Gly*	L	6193-6261	69			12
tRNA-*Glu*	L	6274-6338	65			0
12s	H	6339-7296	958			0
tRNA-*Val*	H	7297-7364	68			0
16s	H	7365-8716	1352			0
tRNA-*Leu*	H	8717-8785	69			2
tRNA-*Leu*	H	8788-8856	69			0
Nad1	H	8857-9798	942	ATG	TAG	6
tRNA-*Pro*	H	9805-9872	68			1
Nad6	H	9874-10374	501	ATG	TAA	6
Cytb	H	10381-11520	1140	ATG	TAA	10
tRNA-*Ser*	H	11531-11595	65			-1
tRNA-*Thr*	L	11595-11664	70			18
Nad4L	H	11683-11979	297	ATG	TAG	11
Nad4	H	11991-13346	1356	ATA	TAG	-1
tRNA-*His*	H	13346-13412	67			1
Nad5	H	13414-15135	1722	ATG	TAG	32
tRNA-*Phe*	H	missing	—			—

Tritia elongata 15,145 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-752	incomplete	—	TAA	12
tRNA-*Lys*	H	765-831	67			-1
tRNA-*Ala*	H	831-900	70			7
tRNA-*Arg*	H	908-978	71			2
tRNA-*Asn*	H	981-1047	67			14
tRNA-*Ile*	H	1062-1129	68			3
Nad3	H	1133-1486	354	ATG	TAG	0
tRNA-*Ser*	H	1487-1554	68			0
Nad2	H	1555-2609	1055	ATG	TA	0
Cox1	H	2610-4145	1536	ATG	TAA	29
Cox2	H	4175-4861	687	ATG	TAA	-2
tRNA-*ASp*	H	4860-4927	68			1
Atp8	H	4929-5087	159	ATG	TAA	7
Atp6	H	5095-5790	696	ATG	TAA	38
tRNA-*Met*	L	5829-5895	67			1
tRNA-*Tyr*	L	5897-5968	72			-1
tRNA-*Cys*	L	5968-6032	65			0
tRNA-*Trp*	L	6033-6098	66			-3
tRNA-*Gln*	L	6096-6162	67			0
tRNA-*Gly*	L	6163-6231	69			12
tRNA-*Glu*	L	6244-6308	65			0
12s	H	6309-7267	959			0
tRNA-*Val*	H	7268-7335	68			0
16s	H	7336-8686	1351			0
tRNA-*Leu*	H	8687-8756	70			1
tRNA-*Leu*	H	8758-8828	71			-1
Nad1	H	8828-9769	942	ATG	TAG	6
tRNA-*Pro*	H	9776-9843	68			1
Nad6	H	9845-10345	501	ATG	TAA	5
Cytb	H	10351-11490	1140	ATG	TAA	8
tRNA-*Ser*	H	11499-11569	71			-2
tRNA-*Thr*	L	11568-11635	68			19
Nad4L	H	11655-11951	297	ATG	TAG	11
Nad4	H	11963-13318	1356	ATA	TAG	-1
tRNA-*His*	H	13318-13382	65			0
Nad5	H	13383-15104	1722	ATG	TAG	41
tRNA-*Phe*	H	missing	—			—

Tritia ephamilla 15,186 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-776	incomplete	—	TAA	15
tRNA-*Lys*	H	792-856	65			1
tRNA-*Ala*	H	858-925	68			9
tRNA-*Arg*	H	935-1003	69			9
tRNA-*Asn*	H	1013-1080	68			18
tRNA-*Ile*	H	1099-1166	68			3
Nad3	H	1170-1523	354	ATG	TAA	-1
tRNA-*Ser*	H	1523-1592	70			-1
Nad2	H	1592-2646	1055	ATG	TA	0
Cox1	H	2647-4182	1536	ATG	TAA	27
Cox2	H	4210-4896	687	ATG	TAA	-2
tRNA-*Asp*	H	4895-4962	68			1
Atp8	H	4964-5122	159	ATG	TAA	7
Atp6	H	5130-5825	696	ATG	TAA	43
tRNA-*Met*	L	5869-5935	67			2
tRNA-*Tyr*	L	5938-6003	66			1
tRNA-*Cys*	L	6005-6069	65			0
tRNA-*Trp*	L	6070-6135	66			-3
tRNA-*Gln*	L	6133-6199	67			-1
tRNA-*Gly*	L	6199-6267	69			13
tRNA-*Glu*	L	6281-6345	65			0
12s	H	6346-7301	956			0
tRNA-*Val*	H	7302-7369	68			0
16s	H	7370-8719	1350			0
tRNA-*Leu*	H	8720-8788	69			2
tRNA-*Leu*	H	8791-8861	71			-1
Nad1	H	8861-9802	942	ATG	TAA	6
tRNA-*Pro*	H	9809-9876	68			1
Nad6	H	9878-10378	501	ATG	TAA	4
Cytb	H	10383-11522	1140	ATG	TAA	16
tRNA-*Ser*	H	11539-11603	65			-1
tRNA-*Thr*	L	11603-11673	71			20
Nad4L	H	11694-11990	297	ATG	TAG	11
Nad4	H	12002-13357	1356	ATA	TAG	-1
tRNA-*His*	H	13357-13422	66			1
Nad5	H	13424-15145	1722	ATG	TAG	41
tRNA-*Phe*	H	missing	—			—

Tritia grana 15,198 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-770	incomplete	—	TAA	15
tRNA-*Lys*	H	786-850	65			1
tRNA-*Ala*	H	851-918	68			9
tRNA-*Arg*	H	928-996	69			16
tRNA-*Asn*	H	1013-1080	68			12
tRNA-*Ile*	H	1093-1160	68			3
Nad3	H	1164-1517	354	ATG	TAG	0
tRNA-*Ser*	H	1518-1585	68			0
Nad2	H	1586-2641	1056	ATG	TAA	0
Cox1	H	2642-4177	1536	ATG	TAA	28
Cox2	H	4206-4892	687	ATG	TAA	-2
tRNA-*Asp*	H	4891-4958	68			1
Atp8	H	4960-5118	159	ATG	TAA	7
Atp6	H	5126-5821	696	ATG	TAA	41
tRNA-*Met*	L	5863-5929	67			2
tRNA-*Tyr*	L	5932-5999	68			1
tRNA-*Cys*	L	6001-6066	66			0
tRNA-*Trp*	L	6067-6132	66			1
tRNA-*Gln*	L	6134-6195	62			1
tRNA-*Gly*	L	6197-6264	68			12
tRNA-*Glu*	L	6277-6341	65			0
12s	H	6342-7302	961			0
tRNA-*Val*	H	7303-7370	68			0
16s	H	7371-8720	1350			0
tRNA-*Leu*	H	8721-8789	69			2
tRNA-*Leu*	H	8792-8860	69			0
Nad1	H	8861-9802	942	ATG	TAA	6
tRNA-*Pro*	H	9809-9876	68			1
Nad6	H	9878-10378	501	ATG	TAA	18
Cytb	H	10397-11536	1140	ATG	TAA	12
tRNA-*Ser*	H	11549-11614	66			0
tRNA-*Thr*	L	11615-11682	68			23
Nad4L	H	11706-12002	297	ATG	TAG	11
Nad4	H	12014-13369	1356	ATA	TAG	-1
tRNA-*His*	H	13369-13434	66			1
Nad5	H	13436-15157	1722	ATG	TAG	41
tRNA-*Phe*	H	missing	—			—

Tritia incrassata-Norway 15,170 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-772	incomplete	—	TAA	14
tRNA-*Lys*	H	787-851	65			1
tRNA-*Ala*	H	853-920	68			9
tRNA-*Arg*	H	930-998	69			7
tRNA-*Asn*	H	1006-1072	67			15
tRNA-*Ile*	H	1088-1154	67			3
Nad3	H	1158-1511	354	ATG	TAA	0
tRNA-*Ser*	H	1512-1579	68			0
Nad2	H	1580-2634	1055	ATG	TA	0
Cox1	H	2635-4170	1536	ATG	TAG	28
Cox2	H	4199-4885	687	ATG	TAA	-2
tRNA-*Asp*	H	4884-4951	68			1
Atp8	H	4953-5111	159	ATG	TAA	7
Atp6	H	5119-5814	696	ATG	TAA	41
tRNA-*Met*	L	5856-5922	67			5
tRNA-*Tyr*	L	5928-5994	67			1
tRNA-*Cys*	L	5996-6061	66			0
tRNA-*Trp*	L	6062-6127	66			1
tRNA-*Gln*	L	6129-6190	62			1
tRNA-*Gly*	L	6192-6258	67			13
tRNA-*Glu*	L	6272-6336	65			0
12s	H	6337-7292	956			0
tRNA-*Val*	H	7293-7360	68			0
16s	H	7361-8711	1351			0
tRNA-*Leu*	H	8712-8780	69			2
tRNA-*Leu*	H	8783-8851	69			0
Nad1	H	8852-9793	942	ATG	TAG	6
tRNA-*Pro*	H	9800-9867	68			1
Nad6	H	9869-10369	501	ATG	TAA	4
Cytb	H	10374-11513	1140	ATG	TAA	11
tRNA-*Ser*	H	11525-11590	66			0
tRNA-*Thr*	L	11591-11658	68			19
Nad4L	H	11678-11974	297	ATG	TAG	11
Nad4	H	11986-13341	1356	ATA	TAA	1
tRNA-*His*	H	13343-13407	65			0
Nad5	H	13408-15129	1722	ATG	TAG	41
tRNA-*Phe*	H	missing	—			—

Tritia incrassata-Spain 15,159 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-775	incomplete	—	TAA	14
tRNA-*Lys*	H	790-854	65			1
tRNA-*Ala*	H	856-923	68			9
tRNA-*Arg*	H	933-1001	69			7
tRNA-*Asn*	H	1009-1075	67			15
tRNA-*Ile*	H	1091-1157	67			3
Nad3	H	1161-1514	354	ATG	TAA	0
tRNA-*Ser*	H	1515-1582	68			0
Nad2	H	1583-2637	1055	ATG	TA	0
Cox1	H	2638-4173	1536	ATG	TAG	27
Cox2	H	4201-4887	687	ATG	TAA	-2
tRNA-*Asp*	H	4886-4953	68			1
Atp8	H	4955-5113	159	ATG	TAA	7
Atp6	H	5121-5816	696	ATG	TAA	41
tRNA-*Met*	L	5858-5924	67			5
tRNA-*Tyr*	L	5930-5996	67			1
tRNA-*Cys*	L	5998-6062	65			0
tRNA-*Trp*	L	6063-6128	66			1
tRNA-*Gln*	L	6130-6191	62			1
tRNA-*Gly*	L	6193-6259	67			13
tRNA-*Glu*	L	6273-6337	65			0
12s	H	6338-7293	956			0
tRNA-*Val*	H	7294-7361	68			0
16s	H	7362-8712	1351			0
tRNA-*Leu*	H	8713-8781	69			2
tRNA-*Leu*	H	8784-8852	69			0
Nad1	H	8853-9794	942	ATG	TAG	6
tRNA-*Pro*	H	9801-9868	68			1
Nad6	H	9870-10370	501	ATG	TAA	5
Cytb	H	10376-11515	1140	ATG	TAA	11
tRNA-*Ser*	H	11527-11591	65			0
tRNA-*Thr*	L	11592-11659	68			19
Nad4L	H	11679-11975	297	ATG	TAG	11
Nad4	H	11987-13342	1356	ATA	TAA	1
tRNA-*His*	H	13344-13408	65			0
Nad5	H	13409-15130	1722	ATG	TAG	29
tRNA-*Phe*	H	missing	—			—

Tritia mutabilis 15,148 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-750	incomplete	—	TAA	15
tRNA-*Lys*	H	766-830	65			1
tRNA-*Ala*	H	832-899	68			7
tRNA-*Arg*	H	907-975	69			10
tRNA-*Asn*	H	986-1053	68			16
tRNA-*Ile*	H	1070-1137	68			3
Nad3	H	1141-1494	354	ATG	TAA	0
tRNA-*Ser*	H	1495-1562	68			0
Nad2	H	1563-2617	1055	ATG	TA	0
Cox1	H	2618-4153	1536	ATG	TAA	28
Cox2	H	4182-4868	687	ATG	TAA	-2
tRNA-*Asp*	H	4867-4934	68			1
Atp8	H	4936-5094	159	ATG	TAA	7
Atp6	H	5102-5797	696	ATG	TAG	42
tRNA-*Met*	L	5840-5906	67			2
tRNA-*Tyr*	L	5909-5975	67			1
tRNA-*Cys*	L	5977-6042	66			0
tRNA-*Trp*	L	6043-6108	66			1
tRNA-*Gln*	L	6110-6171	62			1
tRNA-*Gly*	L	6173-6239	67			14
tRNA-*Glu*	L	6254-6318	65			0
12s	H	6319-7278	960			0
tRNA-*Val*	H	7279-7346	68			0
16s	H	7347-8699	1353			0
tRNA-*Leu*	H	8700-8768	69			2
tRNA-*Leu*	H	8771-8839	69			0
Nad1	H	8840-9781	942	ATG	TAA	6
tRNA-*Pro*	H	9788-9855	68			1
Nad6	H	9857-10357	501	ATG	TAG	5
Cytb	H	10363-11502	1140	ATG	TAA	10
tRNA-*Ser*	H	11513-11577	65			0
tRNA-*Thr*	L	11578-11645	68			21
Nad4L	H	11667-11963	297	ATG	TAG	11
Nad4	H	11975-13330	1356	ATA	TAG	-1
tRNA-*His*	H	13330-13395	66			1
Nad5	H	13397-15118	1722	ATG	TAG	30
tRNA-*Phe*	H	missing	—			—

Tritia neritea 15,179 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-771	incomplete	—	TAA	15
tRNA-*Lys*	H	787-851	65			0
tRNA-*Ala*	H	852-919	68			9
tRNA-*Arg*	H	929-997	69			16
tRNA-*Asn*	H	1014-1081	68			18
tRNA-*Ile*	H	1100-1167	68			3
Nad3	H	1171-1524	354	ATG	TAA	0
tRNA-*Ser*	H	1525-1592	68			0
Nad2	H	1593-2647	1055	ATG	TA	0
Cox1	H	2648-4183	1536	ATG	TAA	28
Cox2	H	4212-4898	687	ATG	TAA	-2
tRNA-*Asp*	H	4897-4964	68			1
Atp8	H	4966-5124	159	ATG	TAA	7
Atp6	H	5132-5827	696	ATG	TAA	41
tRNA-*Met*	L	5869-5935	67			3
tRNA-*Tyr*	L	5939-6006	68			1
tRNA-*Cys*	L	6008-6071	64			0
tRNA-*Trp*	L	6072-6137	66			1
tRNA-*Gln*	L	6139-6200	62			1
tRNA-*Gly*	L	6202-6268	67			11
tRNA-*Glu*	L	6280-6344	65			0
12s	H	6345-7300	956			0
tRNA-*Val*	H	7301-7368	68			0
16s	H	7369-8720	1352			0
tRNA-*Leu*	H	8721-8789	69			2
tRNA-*Leu*	H	8792-8860	69			0
Nad1	H	8861-9802	942	ATG	TAA	5
tRNA-*Pro*	H	9808-9875	68			1
Nad6	H	9877-10377	501	ATG	TAA	10
Cytb	H	10388-11527	1140	ATG	TAA	8
tRNA-*Ser*	H	11536-11600	65			0
tRNA-*Thr*	L	11601-11667	67			22
Nad4L	H	11690-11986	297	ATG	TAG	11
Nad4	H	11998-13353	1356	ATA	TAG	-1
tRNA-*His*	H	13353-13421	69			1
Nad5	H	13423-15144	1722	ATG	TAG	35
tRNA-*Phe*	H	missing	—			—

Tritia nitida 15,157 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-750	incomplete	—	TAA	12
tRNA-*Lys*	H	763-827	65			1
tRNA-*Ala*	H	829-898	70			6
tRNA-*Arg*	H	905-975	71			8
tRNA-*Asn*	H	984-1051	68			20
tRNA-*Ile*	H	1072-1139	68			3
Nad3	H	1143-1496	354	ATG	TAG	0
tRNA-*Ser*	H	1497-1564	68			0
Nad2	H	1565-2619	1055	ATG	TA	0
Cox1	H	2620-4155	1536	ATG	TAA	26
Cox2	H	4182-4868	687	ATG	TAA	-1
tRNA-*Asp*	H	4868-4935	68			1
Atp8	H	4937-5095	159	ATG	TAA	7
Atp6	H	5103-5798	696	ATG	TAG	43
tRNA-*Met*	L	5842-5908	67			3
tRNA-*Tyr*	L	5912-5982	71			-1
tRNA-*Cys*	L	5982-6045	64			0
tRNA-*Trp*	L	6046-6111	66			-3
tRNA-*Gln*	L	6109-6175	67			-1
tRNA-*Gly*	L	6175-6243	69			14
tRNA-*Glu*	L	6258-6322	65			0
12s	H	6323-7282	960			0
tRNA-*Val*	H	7283-7349	67			0
16s	H	7350-8701	1352			0
tRNA-*Leu*	H	8702-8770	69			1
tRNA-*Leu*	H	8772-8840	69			0
Nad1	H	8841-9782	942	ATG	TAA	5
tRNA-*Pro*	H	9788-9855	68			1
Nad6	H	9857-10357	501	ATG	TAA	6
Cytb	H	10364-11503	1140	ATG	TAA	8
tRNA-*Ser*	H	11512-11576	65			3
tRNA-*Thr*	L	11580-11649	70			18
Nad4L	H	11668-11964	297	ATG	TAG	11
Nad4	H	11976-13331	1356	ATA	TAG	-1
tRNA-*His*	H	13331-13396	66			1
Nad5	H	13398-15119	1722	ATG	TAG	38
tRNA-*Phe*	H	missing	—			—

Tritia pallaryana 15,144 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-753	incomplete	—	TAG	15
tRNA-*Lys*	H	769-833	65			1
tRNA-*Ala*	H	835-902	68			9
tRNA-*Arg*	H	912-980	69			5
tRNA-*Asn*	H	986-1053	68			15
tRNA-*Ile*	H	1069-1136	68			3
Nad3	H	1140-1493	354	ATG	TAA	0
tRNA-*Ser*	H	1494-1561	68			0
Nad2	H	1562-2616	1055	ATG	TA	0
Cox1	H	2617-4152	1536	ATG	TAA	29
Cox2	H	4182-4868	687	ATG	TAA	-2
tRNA-*Asp*	H	4867-4934	68			1
Atp8	H	4936-5094	159	ATG	TAA	7
Atp6	H	5102-5797	696	ATG	TAA	38
tRNA-*Met*	L	5836-5902	67			3
tRNA-*Tyr*	L	5906-5973	68			1
tRNA-*Cys*	L	5975-6039	65			0
tRNA-*Trp*	L	6040-6105	66			-3
tRNA-*Gln*	L	6103-6169	67			-1
tRNA-*Gly*	L	6169-6238	70			10
tRNA-*Glu*	L	6249-6313	65			0
12s	H	6314-7271	958			0
tRNA-*Val*	H	7272-7339	68			0
16s	H	7340-8690	1351			0
tRNA-*Leu*	H	8691-8762	72			1
tRNA-*Leu*	H	8764-8834	71			-1
Nad1	H	8834-9775	942	ATG	TAA	6
tRNA-*Pro*	H	9782-9849	68			1
Nad6	H	9851-10351	501	ATG	TAG	5
Cytb	H	10357-11496	1140	ATG	TAA	10
tRNA-*Ser*	H	11507-11570	64			-1
tRNA-*Thr*	L	11570-11636	67			19
Nad4L	H	11656-11952	297	ATG	TAG	11
Nad4	H	11964-13319	1356	ATA	TAG	-1
tRNA-*His*	H	13319-13383	65			0
Nad5	H	13384-15105	1722	ATG	TAG	39
tRNA-*Phe*	H	missing	—			—

Tritia pellucida 15,175 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-771	incomplete	—	TAA	15
tRNA-*Lys*	H	787-851	65			0
tRNA-*Ala*	H	852-919	68			9
tRNA-*Arg*	H	929-997	69			16
tRNA-*Asn*	H	1014-1081	68			18
tRNA-*Ile*	H	1100-1167	68			3
Nad3	H	1171-1524	354	ATG	TAA	0
tRNA-*Ser*	H	1525-1592	68			0
Nad2	H	1593-2647	1055	ATG	TA	0
Cox1	H	2648-4183	1536	ATG	TAA	28
Cox2	H	4212-4898	687	ATG	TAA	-2
tRNA-*Asp*	H	4897-4964	68			1
Atp8	H	4966-5124	159	ATG	TAA	7
Atp6	H	5132-5827	696	ATG	TAA	41
tRNA-*Met*	L	5869-5935	67			3
tRNA-*Tyr*	L	5939-6006	68			1
tRNA-*Cys*	L	6008-6072	65			0
tRNA-*Trp*	L	6073-6138	66			1
tRNA-*Gln*	L	6140-6201	62			1
tRNA-*Gly*	L	6203-6269	67			11
tRNA-*Glu*	L	6281-6345	65			0
12s	H	6346-7301	956			0
tRNA-*Val*	H	7202-7369	68			0
16s	H	7370-8718	1349			0
tRNA-*Leu*	H	8719-8787	69			2
tRNA-*Leu*	H	8790-8858	69			0
Nad1	H	8859-9800	942	ATG	TAA	5
tRNA-*Pro*	H	9806-9873	68			1
Nad6	H	9875-10375	501	ATG	TAA	10
Cytb	H	10386-11525	1140	ATG	TAA	8
tRNA-*Ser*	H	11534-11598	65			0
tRNA-*Thr*	L	11599-11665	67			22
Nad4L	H	11688-11984	297	ATG	TAG	11
Nad4	H	11996-13351	1356	ATA	TAG	-1
tRNA-*His*	H	13351-13417	67			1
Nad5	H	13419-15140	1722	ATG	TAG	35
tRNA-*Phe*	H	missing	—			—

Tritia pfeifferi 15,142 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-747	incomplete	—	TAA	15
tRNA-*Lys*	H	763-827	65			0
tRNA-*Ala*	H	828-895	68			5
tRNA-*Arg*	H	901-969	69			16
tRNA-*Asn*	H	986-1053	68			14
tRNA-*Ile*	H	1068-1135	68			3
Nad3	H	1139-1492	354	ATG	TAA	0
tRNA-*Ser*	H	1493-1560	68			0
Nad2	H	1561-2615	1055	ATG	TA	0
Cox1	H	2616-4151	1536	ATG	TAA	28
Cox2	H	4180-4866	687	ATG	TAA	-2
tRNA-*Asp*	H	4865-4932	68			1
Atp8	H	4934-5092	159	ATG	TAA	8
Atp6	H	5101-5796	696	ATG	TAA	42
tRNA-*Met*	L	5839-5905	67			1
tRNA-*Tyr*	L	5907-5974	68			1
tRNA-*Cys*	L	5976-6041	66			0
tRNA-*Trp*	L	6042-6107	66			1
tRNA-*Gln*	L	6109-6170	62			1
tRNA-*Gly*	L	6172-6238	67			12
tRNA-*Glu*	L	6251-6315	65			0
12s	H	6316-7271	956			0
tRNA-*Val*	H	7272-7339	68			0
16s	H	7340-8691	1352			0
tRNA-*Leu*	H	8692-8760	69			3
tRNA-*Leu*	H	8764-8832	69			0
Nad1	H	8833-9774	942	ATG	TAA	6
tRNA-*Pro*	H	9781-9848	68			1
Nad6	H	9850-10350	501	ATG	TAA	5
Cytb	H	10356-11495	1140	ATG	TAA	10
tRNA-*Ser*	H	11506-11570	65			0
tRNA-*Thr*	L	11571-11638	68			21
Nad4L	H	11660-11956	297	ATG	TAG	11
Nad4	H	11968-13323	1356	ATA	TAG	-1
tRNA-*His*	H	13323-13388	66			1
Nad5	H	13390-15111	1722	ATG	TAG	31
tRNA-*Phe*	H	missing	—			—

Tritia varicosa 15,142 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-762	incomplete	—	TAA	18
tRNA-*Lys*	H	781-847	67			-1
tRNA-*Ala*	H	847-916	70			0
tRNA-*Arg*	H	917-985	69			20
tRNA-*Asn*	H	1006-1072	67			14
tRNA-*Ile*	H	1087-1154	68			3
Nad3	H	1158-1511	354	ATG	TAA	0
tRNA-*Ser*	H	1512-1579	68			0
Nad2	H	1580-2634	1055	ATG	TA	0
Cox1	H	2635-4170	1536	ATG	TAG	22
Cox2	H	4193-4879	687	ATG	TAA	-2
tRNA-*Asp*	H	4878-4945	68			1
Atp8	H	4947-5105	159	ATG	TAA	7
Atp6	H	5113-5808	696	ATG	TAA	41
tRNA-*Met*	L	5850-5916	67			2
tRNA-*Tyr*	L	5919-5985	67			1
tRNA-*Cys*	L	5987-6051	65			0
tRNA-*Trp*	L	6052-6117	66			-3
tRNA-*Gln*	L	6115-6181	67			0
tRNA-*Gly*	L	6182-6248	67			13
tRNA-*Glu*	L	6262-6326	65			0
12s	H	6327-7283	957			0
tRNA-*Val*	H	7284-7351	68			0
16s	H	7352-8701	1350			0
tRNA-*Leu*	H	8702-8770	69			2
tRNA-*Leu*	H	8773-8841	69			0
Nad1	H	8842-9783	942	ATG	TAA	5
tRNA-*Pro*	H	9789-9856	68			1
Nad6	H	9858-10358	501	ATG	TAA	2
Cytb	H	10361-11500	1140	ATG	TAA	8
tRNA-*Ser*	H	11509-11573	65			-1
tRNA-*Thr*	L	11573-11641	69			20
Nad4L	H	11662-11958	297	ATG	TAG	11
Nad4	H	11970-13325	1356	ATA	TAG	-1
tRNA-*His*	H	13325-13389	65			1
Nad5	H	13390-15111	1722	ATG	TAG	31
tRNA-*Phe*	H	missing	—			—

Tritia tenuicosta 15,169 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-770	incomplete	—	TAA	12
tRNA-*Lys*	H	783-848	66			1
tRNA-*Ala*	H	850-919	70			8
tRNA-*Arg*	H	928-996	69			11
tRNA-*Asn*	H	1008-1074	67			15
tRNA-*Ile*	H	1090-1157	68			3
Nad3	H	1161-1514	354	ATG	TAA	-1
tRNA-*Ser*	H	1514-1583	70			-1
Nad2	H	1583-2637	1055	ATG	TA	0
Cox1	H	2638-4173	1536	ATG	TAA	25
Cox2	H	4199-4885	687	ATG	TAA	-2
tRNA-*Asp*	H	4884-4951	68			1
Atp8	H	4953-5111	159	ATG	TAA	6
Atp6	H	5118-5813	696	ATG	TAA	42
tRNA-*Met*	L	5856-5922	67			3
tRNA-*Tyr*	L	5926-5996	71			-1
tRNA-*Cys*	L	5996-6060	65			0
tRNA-*Trp*	L	6061-6126	66			-3
tRNA-*Gln*	L	6124-6190	67			0
tRNA-*Gly*	L	6191-6257	67			12
tRNA-*Glu*	L	6270-6335	65			0
12s	H	6336-7296	961			0
tRNA-*Val*	H	7297-7364	68			0
16s	H	7365-8716	1352			0
tRNA-*Leu*	H	8717-8785	69			1
tRNA-*Leu*	H	8787-8857	71			-1
Nad1	H	8857-9798	942	ATG	TAA	4
tRNA-*Pro*	H	9803-9870	68			1
Nad6	H	9872-10372	501	ATG	TAA	6
Cytb	H	10379-11518	1140	ATG	TAA	11
tRNA-*Ser*	H	11530-11593	64			-1
tRNA-*Thr*	L	11593-11662	70			24
Nad4L	H	11687-11983	297	ATG	TAG	11
Nad4	H	11995-13350	1356	ATA	TAG	-1
tRNA-*His*	H	13350-13415	66			1
Nad5	H	13417-15138	1722	ATG	TAG	31
tRNA-*Phe*	H	missing	—			—

Tritia unifasciata 15,168 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-771	incomplete	—	TAG	12
tRNA-*Lys*	H	784-848	65			2
tRNA-*Ala*	H	851-918	68			10
tRNA-*Arg*	H	929-997	69			9
tRNA-*Asn*	H	1007-1074	68			17
tRNA-*Ile*	H	1092-1159	68			3
Nad3	H	1163-1516	354	ATG	TAG	0
tRNA-*Ser*	H	1517-1584	68			0
Nad2	H	1585-2639	1055	ATG	TA	0
Cox1	H	2640-4175	1536	ATG	TAA	25
Cox2	H	4201-4887	687	ATG	TAA	-2
tRNA-*Asp*	H	4886-4953	68			1
Atp8	H	4955-5113	159	ATG	TAA	7
Atp6	H	5121-5816	696	ATG	TAA	40
tRNA-*Met*	L	5857-5923	67			2
tRNA-*Tyr*	L	5926-5992	67			1
tRNA-*Cys*	L	5994-6057	64			0
tRNA-*Trp*	L	6058-6123	66			1
tRNA-*Gln*	L	6125-6186	62			1
tRNA-*Gly*	L	6188-6254	67			14
tRNA-*Glu*	L	6269-6333	65			0
12s	H	6334-7292	959			0
tRNA-*Val*	H	7293-7360	68			0
16s	H	7361-8712	1352			0
tRNA-*Leu*	H	8713-8781	69			2
tRNA-*Leu*	H	8784-8852	69			0
Nad1	H	8853-9794	942	ATG	TAA	5
tRNA-*Pro*	H	9800-9867	68			1
Nad6	H	9869-10369	501	ATG	TAA	6
Cytb	H	10376-11515	1140	ATG	TAG	11
tRNA-*Ser*	H	11527-11591	65			0
tRNA-*Thr*	L	11592-11659	68			21
Nad4L	H	11681-11977	297	ATG	TAG	11
Nad4	H	11989-13344	1356	ATA	TAG	-1
tRNA-*His*	H	13344-13408	65			1
Nad5	H	13410-15131	1722	ATG	TAG	37
tRNA-*Phe*	H	missing	—			—

Tritia vaucheri 15,153 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-750	incomplete	—	TAA	13
tRNA-*Lys*	H	764-829	66			4
tRNA-*Ala*	H	834-901	68			8
tRNA-*Arg*	H	910-978	69			5
tRNA-*Asn*	H	984-1052	69			8
tRNA-*Ile*	H	1061-1128	68			3
Nad3	H	1132-1485	354	ATG	TAA	0
tRNA-*Ser*	H	1486-1553	68			0
Nad2	H	1554-2608	1055	ATG	TA	0
Cox1	H	2609-4144	1536	ATG	TAA	29
Cox2	H	4174-4860	687	ATG	TAA	-2
tRNA-*Asp*	H	4859-4926	68			1
Atp8	H	4928-5086	159	ATG	TAA	6
Atp6	H	5093-5788	696	ATG	TAG	40
tRNA-*Met*	L	5829-5895	67			8
tRNA-*Tyr*	L	5904-5970	67			1
tRNA-*Cys*	L	5972-6035	64			0
tRNA-*Trp*	L	6036-6102	67			1
tRNA-*Gln*	L	6104-6165	62			1
tRNA-*Gly*	L	6167-6233	67			13
tRNA-*Glu*	L	6247-6311	65			0
12s	H	6312-7264	953			0
tRNA-*Val*	H	7265-7332	68			0
16s	H	7333-8687	1355			0
tRNA-*Leu*	H	8688-8756	69			4
tRNA-*Leu*	H	8761-8829	69			0
Nad1	H	8830-9771	942	ATG	TAA	6
tRNA-*Pro*	H	9778-9846	69			1
Nad6	H	9848-10348	501	ATG	TAA	12
Cytb	H	10361-11500	1140	ATG	TAA	13
tRNA-*Ser*	H	11514-11578	65			0
tRNA-*Thr*	L	11579-11644	66			20
Nad4L	H	11665-11961	297	ATG	TAG	11
Nad4	H	11973-13328	1356	CTT	TAG	-1
tRNA-*His*	H	13328-13393	66			1
Nad5	H	13395-15116	1722	ATG	TAG	37
tRNA-*Phe*	H	missing	—			—

Tritia elata 15,167 bp

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-767	incomplete	—	TAA	15
tRNA-*Lys*	H	783-848	66			1
tRNA-*Ala*	H	850-919	70			8
tRNA-*Arg*	H	928-996	69			6
tRNA-*Asn*	H	1003-1070	68			18
tRNA-*Ile*	H	1089-1156	68			3
Nad3	H	1160-1513	354	ATG	TAA	-1
tRNA-*Ser*	H	1513-1582	70			-1
Nad2	H	1582-2636	1055	ATG	TA	0
Cox1	H	2637-4172	1536	ATG	TAA	30
Cox2	H	4203-4889	687	ATG	TAA	-2
tRNA-*Asp*	H	4888-4955	68			1
Atp8	H	4957-5115	159	ATG	TAA	6
Atp6	H	5122-5817	696	ATG	TAG	41
tRNA-*Met*	L	5859-5925	67			1
tRNA-*Tyr*	L	5927-5996	70			5
tRNA-*Cys*	L	6002-6066	65			0
tRNA-*Trp*	L	6067-6132	66			-3
tRNA-*Gln*	L	6130-6196	67			0
tRNA-*Gly*	L	6197-6263	67			15
tRNA-*Glu*	L	6279-6343	65			0
12s	H	6344-7295	952			0
tRNA-*Val*	H	7296-7363	68			0
16s	H	7364-8715	1352			0
tRNA-*Leu*	H	8716-8784	69			3
tRNA-*Leu*	H	8788-8858	71			-1
Nad1	H	8858-9799	942	ATG	TAA	6
tRNA-*Pro*	H	9806-9873	68			1
Nad6	H	9875-10375	501	ATG	TAA	5
Cytb	H	10381-11520	1140	ATG	TAA	10
tRNA-*Ser*	H	11531-11595	65			-1
tRNA-*Thr*	L	11595-11664	70			20
Nad4L	H	11685-11981	297	ATG	TAG	11
Nad4	H	11993-13348	1356	ATA	TAG	-1
tRNA-*His*	H	13348-13413	66			1
Nad5	H	13415-15136	1722	ATG	TAG	31
tRNA-*Phe*	H	missing	—			—

Tritia ovoidea partial mt genome

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-778	incomplete	—	TAA	15
tRNA-*Lys*	H	794-859	66			1
tRNA-*Ala*	H	861-928	68			10
tRNA-*Arg*	H	939-1007	69			7
tRNA-*Asn*	H	1015-1082	68			18
tRNA-*Ile*	H	1101-1168	68			3
Nad3	H	1172-1525	354	ATG	TAA	-1
tRNA-*Ser*	H	1525-1594	70			-1
Nad2	H	1594-2648	1055	ATG	TA	0
Cox1	H	2649-4184	1536	ATG	TAA	30
Cox2	H	4215-4901	687	ATG	TAA	-2
tRNA-*Asp*	H	4900-4968	69			0
Atp8	H	4969-5127	159	ATG	TAA	6
Atp6	H	5134-5829	696	ATG	TAA	41
tRNA-*Met*	L	5871-5937	67			1
tRNA-*Tyr*	L	5939-6008	70			6
tRNA-*Cys*	L	6015-6079	65			-2
tRNA-*Trp*	L	6078-6143	66			-1
tRNA-*Gln*	L	6143-6209	67			-1
tRNA-*Gly*	L	6209-6277	69			14
tRNA-*Glu*	L	6292-6356	65			0
12s	H	6357-7313	957			0
tRNA-*Val*	H	7314-7381	68			0
16s	H	7382-8733	1352			0
tRNA-*Leu*	H	8734-8802	69			3
tRNA-*Leu*	H	8806-8876	71			-1
Nad1	H	8876-9817	942	ATG	TAA	6
tRNA-*Pro*	H	9824-9890	67			1
Nad6	H	9892-10392	501	ATG	TAA	5
Cytb	H	10398-11537	1140	ATG	TAA	9
tRNA-*Ser*	H	11547-11611	65			-1
tRNA-*Thr*	L	11611-11679	69			20
Nad4L	H	11700-11996	297	ATG	TAG	11
Nad4	H	12008-13363	1356	ATA	TAG	66
missing tRNA-*His*						
Nad5	H	13430-15057	1628	—	—	0
tRNA-*Phe*	H	missing	—			—

Tritia tingitana partial mt genome

Gene	Strand	Location	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-762	incomplete	—	TAA	12
tRNA-*Lys*	H	775-840	66			0
tRNA-*Ala*	H	841-910	70			6
tRNA-*Arg*	H	917-987	71			8
tRNA-*Asn*	H	996-1065	70			18
tRNA-*Ile*	H	1084-1151	68			3
Nad3	H	1155-1508	354	ATG	TAA	0
tRNA-*Ser*	H	1509-1577	69			-1
Nad2	H	1577-2631	1055	ATG	TA	0
Cox1	H	2632-4167	1536	ATG		28
Cox2	H	4196-4882	687		TAA	-2
tRNA-*Asp*	H	4881-4949	69			0
Atp8	H	4950-5108	159	ATG	TAA	8
Atp6	H	5117-5812	696	ATG	TAG	46
tRNA-*Met*	L	5859-5925	67			2
tRNA-*Tyr*	L	5928-5998	71			-1
tRNA-*Cys*	L	5998-6061	64			-2
tRNA-*Trp*	L	6060-6125	66			-1
tRNA-*Gln*	L	6125-6191	67			-1
tRNA-*Gly*	L	6191-6259	69			11
tRNA-*Glu*	L	6271-6335	65			0
12s	H	6336-7298	963			0
tRNA-*Val*	H	7299-7366	68			0
16s		7367-8725	1359			0
tRNA-*Leu*	H	8726-8796	71			3
tRNA-*Leu*	H	8797-8865	69			0
Nad1	H	8866-9807	942	ATG	TAA	6
tRNA-*Pro*	H	9814-9880	67			1
Nad6	H	9882-10382	501	ATG	TAA	6
Cytb	H	10389-11528	1140	ATG	TAA	10
tRNA-*Ser*	H	11539-11603	65			0
tRNA-*Thr*	L	11604-11671	68			19
Nad4L	H	11691-11987	297	ATG	TAG	11
Nad4	H	11999-13354	1356	ATA	TAG	-1
tRNA-*His*	H	13354-13419	66			1
Nad5	H	13421-15142	1722	ATG	TAG	30
tRNA-*Phe*	H	missing	—			—

Anentome sp. 15,069 bp

Gene	Strand	Lo1cation	Size (bp)	Start Codon	Stop codon	Intergenic nucleotides
Cox3	H	1-766	incomplete	—	TAA	4
tRNA-*Lys*	H	771-838	68			-1
tRNA-*Ala*	H	838-904	67			0
tRNA-*Arg*	H	905-973	69			5
tRNA-*Asn*	H	979-1047	69			6
tRNA-*Ile*	H	1054-1124	71			1
Nad3	H	1126-1479	354	ATG	TAA	10
tRNA-*Ser*	H	1490-1559	70			-1
Nad2	H	1559-2613	1055	ATG	TA	0
Cox1	H	2614-4149	1536	ATG	TAA	15
Cox2	H	4165-4851	687	ATG	TAA	-2
tRNA-*Asp*	H	4850-4917	68			1
Atp8	H	4919-5077	159	ATG	TAA	2
Atp6	H	5080-5772	693	ATG	TAA	31
tRNA-*Met*	L	5804-5868	65			1
tRNA-*Tyr*	L	5869-5934	66			5
tRNA-*Cys*	L	5940-6003	64			44
tRNA-*Gln*	L	6048-6114	67			0
tRNA-*Trp*	L	6115-6180	66			2
tRNA-*Gly*	L	6183-6251	69			-2
tRNA-*Glu*	L	6250-6315	66			0
12s	H	6316-7266	951			0
tRNA-*Val*	H	7267-7336	70			0
16s	H	7337-8671	1335			0
tRNA-*Leu*	H	8672-8741	70			3
tRNA-*Leu*	H	8745-8815	71			-1
Nad1	H	8815-9756	942	ATG	TAA	5
tRNA-*Pro*	H	9762-9828	67			1
Nad6	H	9830-10333	504	ATG	TAA	27
Cytb	H	10361-11500	1140	ATG	TAA	-1
tRNA-*Ser*	H	11500-11565	66			21
Nad4L	H	11587-11883	297	ATG	TAG	5
Nad4	H	11889-13244	1356	TTA	TAA	-1
tRNA-*His*	H	13244-13309	66			0
Nad5	H	13310-15022	1713	ATG	TAA	47
tRNA-*Phe*	H	missing	—			—

Table S4 Pairwise uncorrected sequence divergence within *Tritia*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 *T. neritea*																						
2 *T. pellucida*	0.023																					
3 *T. grana*	0.129	0.128																				
4 *T. pfeifferi*	0.139	0.138	0.152																			
5 *T. mutabilis*	0.128	0.128	0.143	0.143																		
6 *T. pallaryana*	0.143	0.140	0.148	0.153	0.150																	
7 *T. corniculum*	0.143	0.140	0.149	0.154	0.151	0.006																
8 *T. elongata*	0.146	0.146	0.153	0.155	0.150	0.108	0.109															
9 *T. incrassata*-Spain	0.171	0.172	0.179	0.183	0.174	0.185	0.185	0.184														
10 *T. incrassata*-Norway	0.168	0.169	0.177	0.181	0.173	0.183	0.182	0.183	0.038													
11 *T. varicosa*	0.190	0.190	0.195	0.196	0.189	0.199	0.198	0.195	0.186	0.183												
12 *T. cuvierii*	0.151	0.150	0.164	0.167	0.158	0.163	0.163	0.166	0.184	0.179	0.199											
13 *T. tenuicosta*	0.148	0.150	0.160	0.165	0.157	0.166	0.167	0.168	0.177	0.173	0.198	0.125										
14 *T. unifasciata*	0.162	0.161	0.173	0.173	0.168	0.176	0.176	0.176	0.185	0.185	0.192	0.139	0.139									
15 *T. reticulata*	0.152	0.151	0.161	0.165	0.149	0.163	0.165	0.162	0.170	0.168	0.187	0.135	0.133	0.138								
16 *T. nitida*	0.156	0.154	0.162	0.169	0.152	0.164	0.166	0.169	0.171	0.168	0.189	0.133	0.136	0.141	0.106							
17 *T. denticulata*	0.132	0.130	0.147	0.146	0.136	0.143	0.143	0.149	0.164	0.163	0.179	0.135	0.135	0.149	0.135	0.136						
18 *T. ovoidea*	0.136	0.133	0.144	0.150	0.134	0.148	0.148	0.155	0.161	0.160	0.187	0.142	0.141	0.154	0.139	0.139	0.120					
19 *T. tingitana*	0.146	0.146	0.159	0.156	0.152	0.157	0.157	0.163	0.176	0.173	0.192	0.135	0.137	0.151	0.129	0.133	0.130	0.138				
20 *T. ephamilla*	0.130	0.129	0.143	0.148	0.132	0.141	0.142	0.149	0.159	0.158	0.184	0.144	0.142	0.151	0.133	0.137	0.110	0.116	0.134			
21 *T. elata*	0.129	0.127	0.139	0.140	0.129	0.141	0.141	0.150	0.160	0.157	0.181	0.137	0.139	0.149	0.133	0.136	0.113	0.073	0.131	0.110		
22 *I. obsoleta*	0.146	0.144	0.156	0.159	0.151	0.163	0.162	0.165	0.173	0.173	0.188	0.158	0.159	0.170	0.154	0.157	0.138	0.139	0.151	0.134	0.135	
23 *T. vaucheri*	0.160	0.159	0.166	0.171	0.162	0.174	0.174	0.177	0.186	0.184	0.203	0.175	0.175	0.183	0.173	0.172	0.158	0.160	0.166	0.159	0.155	0.166

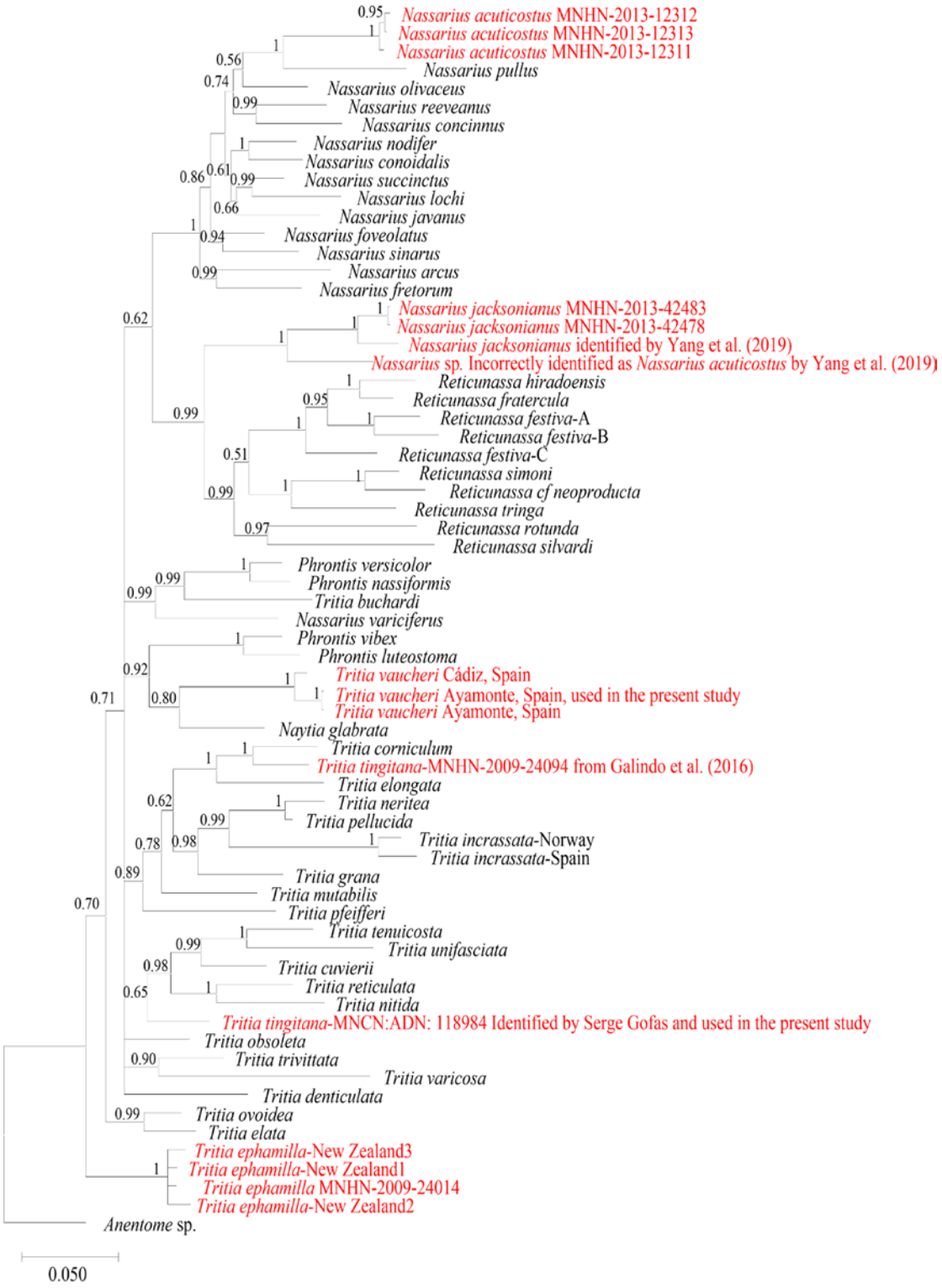


Figure S1. Phylogenetic relationships within Nassarrinae with *Anentome* sp. as outgroup based on the nucleotide sequences of *cox1* fragments. Numbers at nodes are statistical support values for BI (posterior probabilities). For species in red, several specimens were seqeunced to ensure their correct identification.