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Journal of Crustacean Biology, Vol. 10, No. 1. (Feb., 1990), pp. 1-13.

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JOURNAL OF CRUSTACEAN BIOLOGY, 10(1): 1–13, 1990

MOLECULAR PHYLOGENY OF SELECTED DECAPOD CRUSTACEANS BASED ON 18S rRNA NUCLEOTIDE SEQUENCES

Won Kim and Lawrence G. Abele

ABSTRACT

Nucleotide sequences from the 18S subunit of ribosomal RNA were determined for 9 species of decapod crustaceans: 1 from the suborder Dendrobranchiata (*Penaeus aztecus*) and 8 from the suborder Pleocyemata, representing 4 different infraorders (*Procaris ascensionis* and *Palaemonetes kadiakensis,* Caridea; *Stenopus hispidus,* Stenopodidea; *Procambarus leonensis, P. paeninsulanus,* and *P. youngi,* Astacidea; *Callinectes sapidus,* Brachyura). The total aligned set of nucleotides consisted of sequences ranging in length from 869–1721 bases. Comparison of sequences among species revealed that (1) the nucleotide sequences of the 3 species of *Procambarus* are virtually identical, differing in only 3 of more than 1,500 nucleotides; (2) variation is not evenly distributed across the molecule but follows a repeated pattern of conserved region-variable region-highly variable region; (3) the transversion : transition ratio varies from 0.67–1.52, with a mean of 0.987 ± 0.042 across all species; (4) *Penaeus aztecus* differs from the other species in the sequence of a highly conserved region; (5) there is sufficient variation for phylogenetic analysis; and (6) the variation is phylogenetically informative to infraorder or possibly superfamily level. Phylogenetic relationships were inferred by parsimony analysis, and confidence intervals were estimated by bootstrapping. With the brine shrimp *Artemia salina* as an outgroup, the following results were obtained: *Penaeus aztecus* comes off the tree first, followed by a node leading to the remaining decapods; next is a branch leading to a node uniting *Procaris ascensionis* and *Palaemonetes kadiakensis*; the next branch to come off the tree leads to *Stenopus hispidus,* which is followed by a node uniting *Procambarus leonensis* and *Callinectes sapidus.* Bootstrap analyses suggest that both the node uniting *P. kadiakensis* and *P. ascensionis* and that uniting *P. leonensis* and *C. sapidus* are valid. Similar results were obtained with only decapod species using *P. aztecus* as the outgroup. An invariants/operator-metrics analysis supports a *P. kadiakensis/P. ascensionis* and a *S. hispidus/P. leonensis* clade at $P < 0.006$; adding *C. sapidus* supports the placement of *S. hispidus* with reptant taxa.

In the past two decades molecular techniques have been of great value in systematic and evolutionary biology (e.g., Nei, 1987). The greatest progress has occurred in the determination of nucleic acid sequences. This is especially true for the nucleotide sequences of small-subunit (5S, 16S, 18S, etc.) ribosomal RNAs, which have played a major role in the development of phylogenetic ideas concerning prokaryotes (see e.g., Woese, 1987; Lake, 1988) and, more recently, eukaryotes (Field *et al.,* 1988) and pentastome-crustacean relationships (Abele *et al.,* 1989). The development of a rapid and relatively simple method for the determination of partial sequences of rRNA by Lane *et al.* (1985) has greatly advanced progress in molecular phylogenies based on this macromolecule.

The small-subunit rRNA macromolecules have proven to be quite useful in phylogenetic analyses because they are (1) universal, (2) conservative, (3) of a size that yields sufficient data for analysis, (4) functionally constant, and (5) relatively simple to sequence (see e.g., Olsen *et al.,* 1986; Woese, 1987; Field *et al.,* 1988, and references therein), although they alone cannot (nor can any other macromolecule) provide a definitive phylogenetic answer (see e.g., Patterson, 1987; Rothschild *et al.,* 1986).

However, data derived from these molecules can be used as an independent test of phylogenies based on morphological data. Here we use 18S rRNA nucleotide sequences to test ideas on phylogenetic relationships among some groups of Decapoda.

MATERIALS AND METHODS

Materials.—The taxa examined are listed in Table 1.

Methods.—The protocol described below is similar to that of Lane *et al.* (1985) with modifications from Dillon *et al.* (1985) and Maniatis *et al.* (1985), with the additional modification that changing the buffer from Tris/$MgCl_2$/NH_4Cl to ACE (NaOAc/NaCl/Na_2EDTA) during the extraction process greatly increased the amount of RNA extracted per sample. This protocol

works well with fresh material. Recently, we have used it on crustaceans that had been preserved in 100% ethanol and were able to obtain and sequence 18S rRNA from approximately 1.5 g of tissue.

Preparations of rRNA.—Freshly sacrificed specimens or those preserved at −70°C were dissected, and the tissue (about 3 g) was crushed for 5 min in a mortar with 4 μl of human placental RNase inhibitor (1,000 units/100 μl, purchased from BRL Life Technologies, Inc., Baltimore, Maryland) or 0.5 ml VRC (vanadyl ribonucleoside complex, 5 ml/200 mM, from BRL Life Technologies, Inc.), 4 μl of DNase I (2 mg/225 μl, from BRL Life Technologies, Inc.), and 100 μl of 10% SDS (sodium dodecyl sulphate). Acid-washed sand was gradually added during 5 additional min of grinding. The tissue was suspended in a total volume of 10 ml of ACE buffer and ground for a third 5 min. The suspension was transferred to a centrifuge tube, and an equal volume of phenol equilibrated with ACE buffer was added. After the tube was shaken for 30 min on a rotary shaker, the suspension was centrifuged for 15 min at 15,000 *g* at 4°C, and the supernatant was collected. Two more phenol extractions, one with a 1:1 mixture of phenol and CIA (chloroform : isoamyl alcohol at 24:1) and a final extraction with CIA alone, were conducted, after which 2.5 volumes of −20°C absolute ethanol were added to the supernatant and adjustment made to 0.3 M NaOAc. RNA was precipitated for 2 h at −20°C. After centrifugation at 15,000 *g* for 15 min, the RNA pellet was collected, washed with 70% ethanol, and dried. The dried RNA pellet was dissolved in 1 ml of 10 mM Tris·HCl/1 mM EDTA (pH 7.5).

Purification of rRNA.—0.5 ml of the above crude lysate was transferred to a 1.5-ml microcentrifuge tube and incubated at 37°C for 30 min after the addition of 50 μl of 1 M NaOAc/50 mM $MgCl_2$ (pH 5.0), 1 μl of DNase I (2 mg/225 ml) and 1 μl of human placental RNase inhibitor (1,000 units/100 μ1). Incubation at 37°C for another 30 min followed addition of sufficient SDS to make a solution with a final concentration of 0.1% and 1/200 volume of the stock solution of proteinase K (10 mg/ml, purchased from Sigma Chemical Co., St. Louis, Missouri). The RNA was extracted with phenol, a 1:1 mixture of phenol and CIA, and CIA alone. After precipitation with absolute ethanol, the RNA pellet was collected by ethanol centrifugation, washed with 70% EtOH, dried, dissolved in 100 μl of sterile 10 mM Tris·HC1/1 mM EDTA (pH 7.5), and stored at −70°C.

Reverse Transcriptase.—Reverse transcriptase from avian myeloblastosis virus (10,000 units/ml) was purchased from Seikagaku America, Inc., St. Petersburg, Florida.

Primer End Labeling.—The primers used are listed in Table 2. A mixture of about 100 ng of primer, 5 μl of 0.5 M Tris·HCl (pH 7.6)/0.1 M $MgCl_2$/50 mM DTT(dithiothreitol)/1 mM EDTA, 0.3 mCi of 32P gamma ATP, 20 units of T4 kinase (10 units/μl, purchased from BRL Life Technologies, Inc.), and sufficient water to make a total volume of 50 μl was incubated at 37°C for 30 min. A 100-μl DEAE cellulose column was prepared in a 1-ml pipet tip plugged with glass wool. The column was washed with 1 ml of SSC(0.0015 M sodium citrate/0.15 M NaCl)/1 M NaCl and equilibrated with 1 ml of SSC. After loading with the above mixture, the column was washed with 3 ml of SSC and eluted with 300 μl of SSC/1 M NaCl. The end-labeled primer was precipitated with 2.5 volumes of absolute ethanol overnight at −20°C. After spinning for 1 h in an Eppendorf microcentrifuge, the primer pellet was collected, dried, dissolved in 20 μl of 10 mM Tris·HCl/1 mM EDTA (pH 7.5), and stored at −20°C.

RNA Template/Primer Annealing Reaction.—1.5 μl of 500 mM KCl/250 mM Tris·HCl (pH 8.5), 3.5 μl of RNA (2 μg/μl), and 2.5 μl of primer were mixed in a microcentrifuge tube. After centrifugation for 5 s, the reaction mixture was kept at 80°C for 1 min and transferred quickly to a covered 65°C water bath. After addition of 1 μl of human placental RNase inhibitor (1,000 units/100 μl), the water bath was turned off and allowed to cool to room temperature. The tube containing the annealing reaction mixture was then centrifuged for 5 s in a microcentrifuge.

Prereaction Mixture.—6.5 μl of the above hybridization (annealing) mixture containing the 5′ end-labeled primer were transferred to a microcentrifuge tube. The following components were added: 6.5 μl of 250 mM Tris·HCl, pH 8.3/250 mM KCl/50 mM dithiothreitol/50 mM $MgCl_2$, 2 μl of reverse transcriptase (10 units/μl), 3.5 μl of sterile distilled water, 1 μl of human placental RNase inhibitor (0.7 unit/μl). The mixture was then spun for 5 s in an Eppendorf microcentrifuge.

Reaction Mixture.—4 μl of the prereaction mixture was transferred to each of four 500-μl microcentrifuge tubes containing 1 μl of a 200-μM dNTP mix (dATP, dCTP, dGTP, dTTP) and 1 μl of a particular ddNTP calculated to produce the following ratios: ddATP/dATP = 1.3; ddCTP/dCTP = 0.4; ddGTP/dGTP = 0.3; ddTTP/dTTP = 0.9. The components were mixed, spun for 5 s in a microcentrifuge, placed in a 46°C water bath for 1 h, and dried in a speedvac (Savant Instruments, Inc., Farmingdale, New York). After addition of 6 μl of 86% formamide/10 mM EDTA/0.08% xylene cyanol/0.08% bromophenol blue, each tube was placed in a 100°C water bath for 2 min, quenched in ice water for 3 min, and spun for 5 s in a microcentrifuge. The samples were loaded onto a sequencing gel or stored at −70°C.

Electrophoresis.—An 8% polyacrylamide gel mixture (15 ml of acrylamide/bis (19:1, w/w) 40% stock, 34.5 g of urea, 15 ml of 5xTBE, distilled water to total volume 75 ml, 110 μl of 25% ammonium persulfate, 110 μl of TEMED) was poured between two 30 × 40-cm glass plates spaced 0.4 mm apart. The gel was pre-electrophoresed for 30 min at a minimum of 1,500 V before sample loading. A 3-μl sample of each reaction was loaded into a well of the shark-tooth comb, and electrophoresis proceeded for approximately 1.5 h at 65 W, 1,500–1,800 V, 40–50 mA, until the first dye band (bromophenol blue) reached the bottom of the gel. A second loading was run for approximately another 1.5 h. The gel was removed from the glass plates, fixed for 20 min in 2 l of 5% methanol/5% glacial acetic acid solution, transferred to 3-mm Whatman filter paper, and dried for 1 h in a gel dryer. The gel was exposed to Kodak XAR–5 film (or Dupont Cronex 35.6 × 43.2-cm film) for 24–48 h at room temperature, after which the film was developed.

Analysis.—There is no agreement on methods for inferring phylogenetic relationships among taxa on the

Table 1. A list of species sequenced for this study.

Taxa	Number of nucleotides
Decapoda	
Suborder Dendrobranchiata	
Family Penaeidae	
Penaeus aztecus Ives	1,301
Suborder Pleocyemata	
Infraorder Caridea	
Family Procarididae	
Procaris ascensionis Chace and Manning	869
Family Palaemonidae	
Palaemonetes kadiakensis Rathbun	1,153
Infraorder Stenopodidea	
Family Stenopodidae	
Stenopus hispidus (Olivier)	1,315
Infraorder Astacidea	
Family Cambaridae	
Procambarus leonensis Hobbs	1,721
P. youngi Hobbs	1,531
P. paeninsulanus (Faxon)	1,587
Infraorder Brachyura	
Family Portunidae	
Callinectes sapidus Rathbun	1,182

basis of nucleotide sequences (see e.g., Felsenstein, 1988a, b; Lake, 1988; Olsen, 1987, 1988). The approaches can be classified as (1) distance matrix techniques, (2) parsimony methods, (3) maximum-likelihood methods, and (4) invariant/operator-metrics methods. For the present study we used parsimony methods for most analyses.

Alignment.—The alignment of multiple ($N > 2$) sequences represents a major problem in deriving sequence-based phylogenies because there is no accepted algorithm, and the alignment determines, to a large extent, the inferred phylogeny (see Sankoff *et al.*, 1973; Howqeweg and Hesper, 1984; Feng and Doolittle, 1987; Felsenstein, 1988a). We examined this problem in several ways during the present study. We first aligned all species against *Artemia salina* because the complete sequence is available for this species. We also aligned all species against *Procambarus leonensis,* beginning with the most similar species (*Callinectes sapidus*) as determined by pairwise comparisons excluding the nearly identical congeneric species of *Procambarus* (Table 3). For these alignments we used the MicroGenie® (see Cannon, 1987; von Heijne, 1988) algorithm, which maximizes the value S, where S = M–G–N (M = matches, G = gaps, N = number of residues in the gaps). These two alignments differed in the number and location of phylogenetically informative sites (and alignment gaps) and hence yielded different inferred phylogenies. We repeated the alignments using the Needleman and Wunsch (1970) procedure (which is based on a matrix scoring system) in the FASTA program of Pearson and Lipman (1988). These alignments also differed from each other and from the previous alignments. All alignments were compared by means of REDUCSEQ by Dr. David Swofford. This program produces a file (file.lst) that numbers and identifies all sites as being invariant, variable but uninformative, or variable and phylogenetically informative. This allows a site by site comparison among the various alignments. The procedure was repeated coding alignment gaps as characters and as unknown. Each data set was analyzed using PAUP (Swofford, 1985), and the results compared. A new data set was also generated that was derived using only those sites that were both informative and common to all alignments. The various phylogenies, using *A. salina* as an outgroup, differed only in the placement of *Stenopus hispidus*; this species grouped as shown in Fig. 2 or along the branch leading to *Procaris ascensionis* and *Palaemonetes kadiakensis.* This ambiguity in the placement of *S. hispidus* is also reflected in the bootstrap analysis (see Fig. 2). All analyses, however, yielded the same result if *Artemia salina* was not included and *Penaeus aztecus* was used as the outgroup (see Results). The alignment shown in Appendix I is that based on FASTA, beginning with the most similar species pair (*P. leonensis* and *C. sapidus*).

The Data

The total aligned set of nucleotides consisted of sequences ranging in length from 869–1,721 bases (Table 1, Appendix 1) excluding alignment gaps and unreadable regions (sites where there is evidence of a nucleotide but the autoradiogram is not clear enough to read with confidence). We indicated unreadable sites with an N if a band was present in all four lanes and if sequence information from another species suggested a base at that site. For all analyses we scored N = ?. The sequences will be deposited in GenBank, Los Alamos National Laboratory, Los Alamos, New Mexico.

For the maximum-parsimony analyses using PAUP (Swofford, 1985) we first used REDUCSEQ (by David Swofford) to reduce the data set to only those sites that were phylogenetically informative under the parsimony criterion (see Alignment, above). This reduced data set consisted of 156 nucleotides if *Artemia salina* and alignment gaps were included, whereas excluding *A. salina* resulted in 96 informative sites. The limited number of taxa permitted the use of the ALLTREES option.

For the initial analyses we used the branchiopod *Artemia salina* as an outgroup based on the sequence published by Nelles *et al.* (1984). These analyses revealed two clades, one containing *P. aztecus* and the other containing the remaining decapods. This result is also supported by differences in a highly conserved "primer" region between *P. aztecus* and the remaining decapods (see below). We therefore excluded *A. salina* and

Table 2. A list of oligonucleotide primers used as hybridizing sites to derive c-DNA sequences of 18S rRNA in Crustacea.*

Human c-DNA of 18S rRNA position	Primer
32–46	5′ ACC TTG TTA CGA CTT 3′
162–176	5′ ACG GGC GGT GTG TAC 3′
257–274	5′ CCC GMT CCY CCT CTC GGA 3′
361–375	5′ TCT AAG GGC ATC ACA 3′
481–495	5′ TCT CGT TCG TTA TCG 3′
662–681	5′ CCG TCA AWT YCY TTD RRK TTT 3′
779–793	5′ GCA TCG TTT AHG GTY 3′
897–911	5′ TCC AAG AAT TTC ACC 3′
1053–1067	5′ TAA TTT TTT CAA AGT 3′
1237–1254	5′ GWA TTA CCG CGG CKG CTG 3′
1453–1467	5′ ATT CCC CGT TAC CCG 3′
1700–1714	5′ ACG TCT AGA ATT ACC 3′

* Symbols from Bishop *et al.* (1987, table 1). Each mixture primer site has been verified against a "pure" primer.

used *P. aztecus* as the outgroup in additional analyses.

A pairwise comparison of the taxa is presented in Table 3, where it can be seen that the ratio of transitions to transversions is 0.986 ± 0.042, a value considerably less than the 2.0 characteristic of mammals (see e.g., Nei, 1987). Unfortunately, the fossil record for these taxa (Schram, 1986) is insufficient to warrant any estimate of substitution saturation or divergence of nucleotide sequences as a function of time.

Determining the value of 18S rRNA in phylogenetic studies requires an understanding of its levels of variation. That is, there should be some relationship between nucleotide differences among species and phylogenetic distance as indicated by evidence other than nucleotide sequences. We therefore began with a comparison of the nucleotide sequences of three species in the crayfish genus *Procambarus,* where we expected to find few, if any, differences among the sequences. The sequences were virtually identical: three bases (two insertions, C at site 680 and U at 1438, and two transitions at sites 731 and 732 between *P. leonensis* and *P. youngi* and only the transitions at sites 731 and 732 between *P. leonensis* and *P. paeninsulanus*) out of approximately 1,500 differed among the three species. At a higher taxonomic level, we compared the nucleotide sequences of species considered by morphological criteria (see Burkenroad, 1963; Felgenhauer and Abele, 1983) to represent different suborders within the Decapoda, *Penaeus aztecus* (Dendrobranchiata) and *Stenopus hispidus* (Pleocyemata).

Table 3. Pairwise comparison of the taxa considered in this study. Lower left are raw differences with transitions over transversions. Upper right are raw distances with distances corrected by the method of Jukes and Cantor (1969) in parentheses. N = number of nucleotides. *Procambarus* = *P. leonensis.*

	Artemia	*Penaeus*	*Palaemonetes*	*Procaris*	*Stenopus*	*Procambarus*	*Callinectes*
Artemia	—	0.174 (0.198)	0.181 (0.207)	0.143 (0.159)	0.139 (0.154)	0.131 (0.144)	0.125 (0.137)
Penaeus	122/135	—	0.129 (0.141)	0.126 (0.138)	0.126 (0.138)	0.121 (0.132)	0.110 (0.119)
Palaemonetes	105/148	82/98	—	0.094 (0.101)	0.112 (0.121)	0.126 (0.138)	0.113 (0.122)
Procaris	99/80	67/91	48/70	—	0.110 (0.119)	0.094 (0.101)	0.076 (0.080)
Stenopus	106/101	84/103	79/78	65/73	—	0.093 (0.100)	0.084 (0.089)
Procambarus	135/89	91/88	98/88	64/54	56/83	—	0.038 (0.039)
Callinectes	111/83	68/95	75/83	54/41	55/70	34/25	—

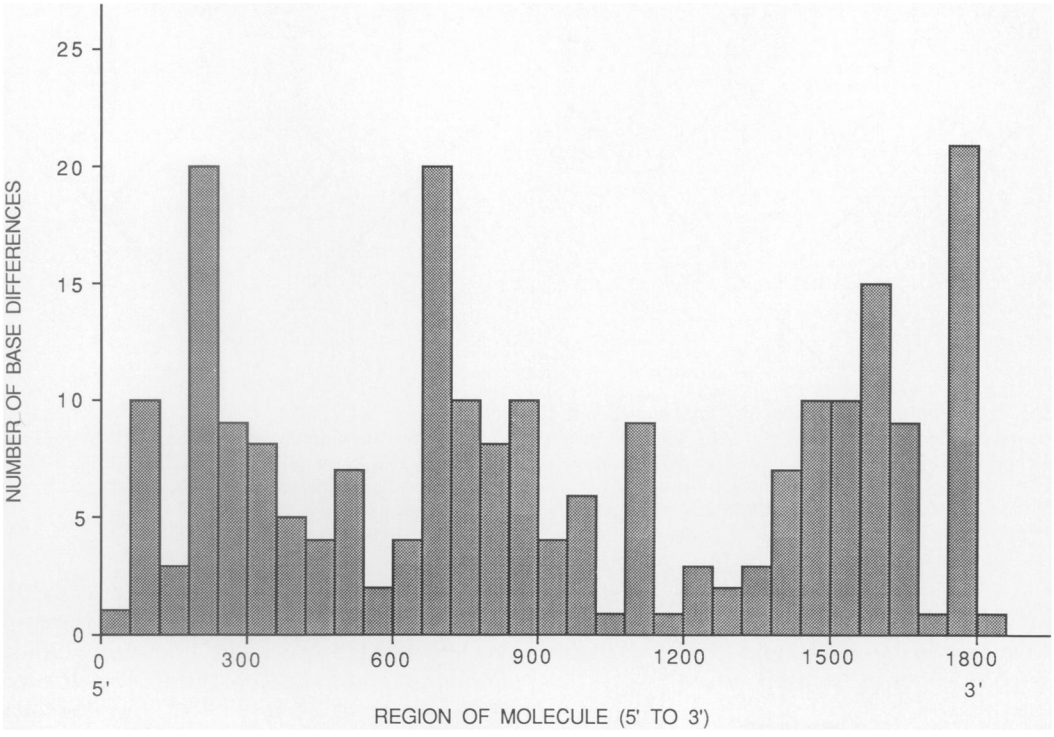

Fig. 1. Number of nucleotide differences (plotted every 60 bases, excluding gaps and insertions) between *Procambarus leonensis* and *Artemia salina* from the 5′ to the 3′ end of the 18S rRNA macromolecule.

These taxa differed at 187 sites among 1,153 bases in common (Table 3) and in the sequence of one primer (positions 1237–1254, Table 2), a highly conserved region that is characteristic of the Pleocyemata. Finally, we compared nucleotide sequences between species at the class level by comparing *Artemia salina* (Branchiopoda) and *Procambarus leonensis* (Malacostraca). There were numerous differences, for example, at the following positions (numbers refer to positions of *A. salina*): 71–77 (6 transversions, 1 transition), 179–181, 222–224, 356–359, 952–955, 1486–1489, 1689–1692, and the region beyond 1700. Compared to *A. salina, P. leonensis* had at least 16 insertions between the members of the following pairs of positions: 23–24, 124–125, 126–127, 230–231, 239–240, 283–284, 426–427, 707–708, 1370–1371, 1381–1382, 1385–1386, 1488–1489, 1526–1527, 1532–1533, 1561–1562, and 1688–1689. The number of nucleotide insertions varied between 1 and 4, although an unreadable region around positions 738–740 suggested a long insertion of perhaps 15 nucleotides. These differences in primary structure of 18S rRNA between *A. salina* and *P. leonensis* are plotted (every 60 bases) from the 5′ to the 3′ end in Fig. 1, where it can be seen that variation is not evenly distributed throughout the molecule. (A plot of any other species would yield a similar pattern.) As in other taxa (Lane *et al.*, 1985), a highly conserved region is followed by a less conserved region that is followed by a variable region, and this pattern is repeated several times across the molecule. The variable regions in decapod crustaceans correspond generally to those regions identified by Nelles *et al.* (1984, fig. 5a, b) as being variable in *A. salina* compared to other eukaryotes. For example, the V7 region near the 3′ end of the molecule contains almost 21% of the variation (between *A. salina* and *P. leonensis*), while the V2 (especially E9–1) and V4 (E19–1) regions account for an additional 26% of the differences.

Two points seem clear: (1) there is suffi-

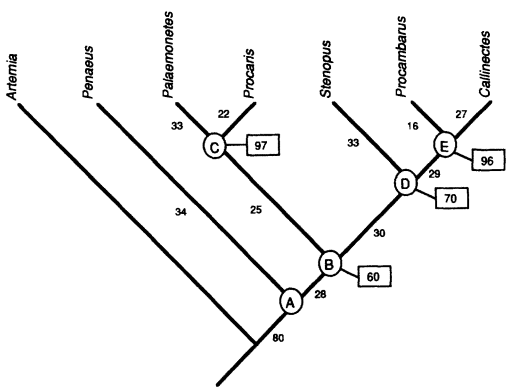

Fig. 2. Relationships among the taxa considered as estimated by PAUP using the ALLTREES option. Length = 357, CI = 0.706, based on 156 characters. □ = An estimate of the confidence intervals of the tree by the bootstrap method based on 100 replicates.

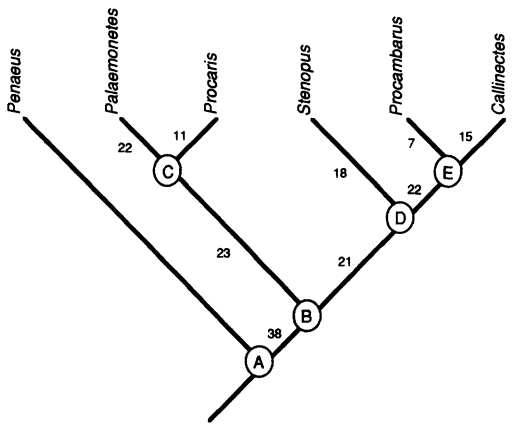

Fig. 3. Relationship among the taxa indicated as estimated by PAUP using the ALLTREES option. Length = 177, CI = 0.740, based on 96 characters.

cient variation in this macromolecule to allow rigorous analysis, and (2) the variation is phylogenetically informative.

Results

Maximum parsimony analysis yielded a single minimum-length tree (Fig. 2) using the ALLTREES option of PAUP. The total length of the tree was 357 steps with a consistency index of 0.706 based on 156 informative sites. *Penaeus aztecus* came off the tree first and was isolated from the remaining species by a branch (A to B) of 28 steps. The second branch (B to C) led to a node (C) that united *Palaemonetes kadiakensis* and *Procaris ascensionis,* suggesting strongly that the Procarididae belong within the Caridea. There was a branch (B to D) of length 25 before the next species, *Stenopus hispidus,* came off the tree. The last two species, *Procambarus leonensis* and *Callinectes sapidus,* came off node E together.

A problem with maximum parsimony is that the result lacks confidence intervals. One way to estimate confidence intervals is the bootstrap method (Felsenstein, 1985), which involves sampling the original data set with replacement. Thus, if bootstrapping resulted in the occurrence of a branch in 95% or more of the bootstrap estimates, we considered that branch to be statistically significant. The results of such an analysis using DNABOOT of PHYLIP (Fig. 2) with *A. salina* as the outgroup suggests that the branch containing *Penaeus aztecus* is weakly distinct from that containing the remaining species. However, the branch including *Palaemonetes kadiakensis* and *Procaris ascensionis* occurred in 97% of the replicates and was unlikely to be the result of chance alone. The branch leading to *S. hispidus, P. leonensis,* and *C. sapidus* occurred in 70% of the replicates, and that containing *P. leonensis* and *C. sapidus* occurred in 96% of the replicates.

Both the parsimony and the bootstrap analyses were repeated after *A. salina* was removed. The results were similar to those described above (Figs. 3, 4), although the bootstrap analysis indicates stronger support for the node leading to *S. hispidus.*

Several authors have suggested different relationships for *S. hispidus,* and we calculated various tree lengths, using DNAMOVE of PHYLIP to move *S. hispidus* to different branches of the tree. The tree in Fig. 2 is 357 steps long; switching *S. hispidus* and *P. leonensis* increased the tree length by 8 steps; moving *S. hispidus* to between nodes A and B resulted in an increase of 7 steps; and moving *S. hispidus* onto branch B–C increased the length 10 steps. Similar results were obtained when the analysis was repeated without *A. salina.* These results are consistent with the above parsimony and bootstrap analyses.

Another approach to examining the placement of *S. hispidus* is to use the techniques of invariants/operator metrics (Lake,

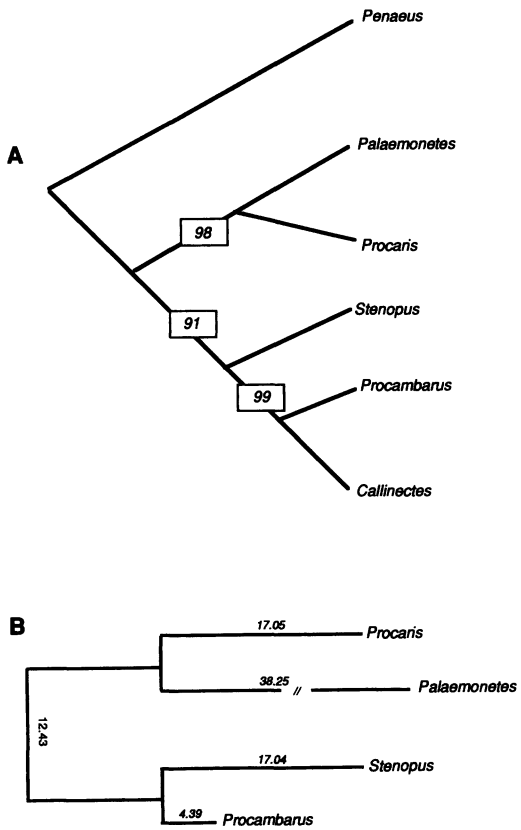

Fig. 4. A. An estimate of the confidence intervals of the tree in Fig. 4 by the bootstrap method based on 100 replicates. B. Relationships as suggested by the method of invariants/operator metrics; branch lengths indicated are average number of transversions per 1,000 nucleotides estimated by operator metrics; for this invariant (X = E + u–H–J = 9 + 2–0–1), the hypothesis is a two-tailed binomial, E + u = H + J where P(E + u; E + u + H + J, 0.5) = P(11; 12, 0.5) = 0.006.

1987a, b). This technique examines patterns of nucleotide differences among four taxa at a time and differentiates between phylogenetically informative and phylogenetically misleading patterns (see Holmquist *et al.*, 1988). The result strongly supports the placement of *S. hispidus* as shown in Figs. 2–4, i.e., distinct from the Caridea and related to reptant taxa. The specific result (Fig. 4B) with reference to *S. hispidus, Procambarus leonensis, Procaris ascensionis,* and *Palaemonetes kadiakensis* is highly significant ($P < 0.006$) and recognizes a *Stenopus/Procambarus* and a *Procaris/Palaemonetes* clade. For this invariant (X = E + u–H–J = 9 + 2–0–1) the hypothesis is a two-tailed binomial, E + u = H + J where P(E + u; E + u + H + J, 0.5) = 0.006. Adding *Callinectes sapidus* to the analysis does not change the result, which is significant ($P < 0.003$) under the same hypothesis and recognizes a *Procaris/Palaemonetes* clade and a *Stenopus/Procambarus/ Callinectes* clade.

In summary, the nucleotide sequences of 18S rRNA, under both parsimony and invariants/operator-metrics analyses, provide support for the recognition of two suborders of the Decapoda and, within the Pleocyemata, for the Caridea, Stenopodidea, Astacoidea, and Brachyura, although the relationships among the latter three groups are not clear-cut.

Discussion

There has been considerable discussion, summarized by Felgenhauer and Abele (1983), of the classification and phylogeny of the Decapoda during the past 25 years. Abundant morphological, embryological, and now molecular data support the recognition of two suborders within the decapods, the Dendrobranchiata and the Pleocyemata (see Burkenroad, 1963, 1981; Schram, 1984; Abele and Felgenhauer, 1986). Current questions on classification and relationships center on groups in the suborder Pleocyemata. For example, several authors have dealt with the placement of the interesting anchialine shrimp *Procaris ascensionis,* described by Chace and Manning (1972), who placed the species in its own family (Procarididae) and superfamily within the Caridea. Kensley and Williams (1986) described a new genus and species of procaridid shrimp (*Vetericaris chaceorum*) and reviewed the literature on the relationship of the family. They concluded that procaridids should be retained as a superfamily within the Caridea, although they noted that critical information on reproduction (i.e., whether or not embryos are carried on the pleopods) was lacking. Abele and Felgenhauer (1986) grouped the procaridids with the Caridea, while Schram (1986) recognized two infraorders, the Procarididea and Caridea, within a suborder Eukyphida. Recently, Felgenhauer *et al.* (1988) made the important discovery that *Procaris ascensionis* carries its embryos on the pleopods, thus clearly demonstrating that procaridids are pleocyemates. It is clear that procaridids are related to the carideans, but,

without more morphological as well as molecular data on other carideans, it is premature to remove procaridids from the infraorder Caridea.

Another controversial group is the Stenopodidea. Abele and Felgenhauer (1986) reviewed the earlier literature on this group and performed additional analyses on its phylogenetic relationships. They followed Saint Laurent (in Saint Laurent and Cleva, 1981) and Schram (1984) in placing the Stenopodidea as an independent infraorder more closely related to "reptant" taxa than to either penaeids or carideans. As noted earlier, moving *S. hispidus* to branch A–B on the tree (creating in effect a "natantian" group) increases the total length by seven steps or about 2%, a rather small amount. However, a consideration of morphological characters, specifically the uniramous first pleopods, reduced first abdominal pleuron and trichobranch gills, as well as the invariants analysis, favors the placement of *S. hispidus* as indicated in Figs. 2 and 4, and all analyses reported here support that conclusion. In addition, the difference in a highly conserved region (see Data) between *P. aztecus* and the remaining decapods strongly favors the two-suborder concept. Finally, it is worth noting that, for the groups in common, there is general agreement between results obtained from morphological (Abele and Felgenhauer, 1986) and molecular data.

Additional data are necessary to determine in greater detail the relationships examined here. Specifically, additional species of dendrobranchiates will have to be sequenced to ascertain whether or not *Penaeus aztecus* is representative of the suborder. Sequences of caridean shrimp from other families will provide insight into the relationship of the Procarididae to other carideans, and the inclusion of sequences from more species of "reptant" decapods (see Spears and Abele, 1988) may resolve the relationship of the Stenopodidea to the other decapods, as well as those among the "reptants" themselves.

Acknowledgements

We offer special thanks to Dr. Ben Stulp, of the Department of Molecular Genetics, State University of Gröningen, and Dr. Robert Reeves, of this department, for their patience while teaching us these techniques. Dr. James Lake provided advice as well as a copy of his invariants/operator-metrics program and Dr. George Wilson provided modified versions of PHYLIP. Ms. Tricia Spears and Dr. Joel Martin aided us in laboratory work and, along with Drs. Bruce Felgenhauer and David Swofford, offered constructive criticism of the manuscript. This research was supported by National Science Foundation grant BSR 87-127169.

Literature Cited

Abele, L. G., and B. E. Felgenhauer. 1986. Phylogenetic and phenetic relationships among the lower Decapoda.—Journal of Crustacean Biology 6: 385–400.

———, W. Kim, and B. E. Felgenhauer. 1989. Molecular evidence for inclusion of the phylum Pentastomida in the Crustacea.—Molecular Biology and Evolution 6: 685–691.

Bishop, M. J., M. Ginsburg, C. J. Rawlings, and R. Wakeford. 1987. Molecular sequence databases.—*In:* M. J. Bishop and C. J. Rawlings, eds., Nucleic acid and protein sequence analysis: a practical approach. Pp. 83–113. IRL Press, Oxford University Press, London, England.

Burkenroad, M. D. 1963. The evolution of the Eucarida (Crustacea, Eumalacostraca) in relation to the fossil record.—Tulane Studies in Geology 2: 2–17.

———. 1981. The higher taxonomy and evolution of Decapoda (Crustacea).—Transactions of the San Diego Society of Natural History 19: 251–268.

Cannon, G. C. 1987. Sequence analysis on microcomputers.—Science 238: 97–103.

Chace, F. A., Jr., and R. B. Manning. 1972. Two new caridean shrimps, one representing a new family, from marine pools on Ascension Island (Crustacea: Decapoda: Natantia).—Smithsonian Contributions to Zoology 131: 1–18.

Dillon, J. R., A. Nasim, and E. R. Nestmann, eds. 1985. Recombinant DNA methodology.—John Wiley and Sons, New York, New York. Pp. 1–219.

Felgenhauer, B. E., and L. G. Abele. 1983. Phylogenetic relationships among shrimp-like decapods.—*In:* F. R. Schram, ed., Crustacean issues I. Crustacean phylogeny. Pp. 291–311. A. A. Balkema Publishers, Rotterdam, Netherlands.

———, ———, and W. Kim. 1988. Reproductive morphology of the anchialine shrimp *Procaris ascensionis* (Decapoda: Procarididae).—Journal of Crustacean Biology 8: 333–339.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap.—Evolution 39: 783–791.

———. 1988a. Phylogenies from molecular sequences: inference and reliability.—Annual Review of Genetics 22: 521–565.

———. 1988b. Perils of molecular introspection.—Nature 335: 118.

Feng, D. -F., and R. F. Doolittle. 1987. Progressive sequence alignment as a prerequisite to correct phylogenetic trees.—Journal of Molecular Evolution 25: 351–360.

Field, K. G., G. J. Olsen, D. J. Lane, S. J. Giovannoni, M. T. Ghiselin, E. C. Raff, N. R. Pace, and R. A. Raff. 1988. Molecular phylogeny of the animal kingdom.—Science 239: 748–753.

Holmquist, R., M. M. Miyamoto, and M. Goodman. 1988. Analysis of higher-primate phylogeny from transversion differences in nuclear and mitochon-

drial DNA by Lake's methods of evolutionary parsimony and operator metrics.—Molecular Biology and Evolution 5: 217–236.

Howqeweg, P., and B. Hesper. 1984. The alignment of sets of sequences and the construction of phyletic trees: an integrated method.—Journal of Molecular Evolution 20: 175–186.

Jukes, T. H., and R. C. Cantor. 1969. Evolution of protein molecules.—*In:* H. N. Munro, ed., Mammalian protein metabolism. Pp. 21–132. Academic Press, New York, New York.

Kensley, B., and D. Williams. 1986. New shrimps (families Procarididae and Atyidae) from a submerged lava tube on Hawaii.—Journal of Crustacean Biology 6: 417–437.

Lake, J. 1987a. Determining evolutionary distances from highly diverged nucleic acid sequences: operator metrics.—Journal of Molecular Evolution 26: 59–73.

———. 1987b. A rate-independent technique for analysis of nucleic acid sequences: evolutionary parsimony.—Molecular Biology and Evolution 4: 167–191.

———. 1988. Origin of the eukaryotic nucleus determined by rate-invariant analysis of rRNA sequences.—Nature 331: 184–186.

Lane, D. J., B. Pace, G. J. Olsen, D. A. Stahl, M. L. Sogin, and N. R. Pace. 1985. Rapid determination of 16S ribosomal RNA sequences for phylogenetic analysis.—Proceedings of the National Academy of Sciences, Washington 82: 6955–6959.

Maniatis, T., E. F. Fritsch, and J. Sambrook. 1985. Molecular cloning, a laboratory manual.—Cold Spring Harbor Laboratory, New York, New York. Pp. 1–545.

Needleman, S. B., and C. D. Wunsch. 1970. A general method applicable to the search for similarities in the amino acid sequence of two proteins.—Journal of Molecular Biology 48: 443–453.

Nei, M. 1987. Molecular evolutionary genetics.—Columbia University Press, New York, New York. Pp. 1–512.

Nelles, L., B.-L. Fang, G. Volckaert, A. Vandenberghe, and R. De Wachter. 1984. Nucleotide sequence of a crustacean 18S ribosomal RNA gene and secondary structure of eukaryotic small subunit ribosomal RNAs.—Nucleic Acids Research 12: 8749–8768.

Olsen, G. J. 1987. Earliest phylogenetic branchings: comparing rRNA-based evolutionary trees inferred with various techniques.—*In:* Cold Spring Harbor Symposia on Quantitative Biology 52: 825–837. Cold Spring Harbor Laboratory, New York, New York.

———. 1988. Phylogenetic analysis using ribosomal RNA.—Methods in Enzymology 164: 793—812.

———, D. J. Lane, S. J. Giovannoni, N. R. Pace, and D. A. Stahl. 1986. Microbial ecology and evolution: a ribosomal RNA approach.—Annual Review of Microbiology 40: 337–365.

Patterson, C. 1987. Introduction.—*In:* C. Patterson, ed., Molecules and morphology in evolution: conflict or compromise? Pp. 1–22. Cambridge University Press, London, England.

Pearson, W. R., and D. J. Lipman. 1988. Improved tools for biological sequence comparison.—Proceedings of the National Academy of Sciences, Washington 85: 2444–2448.

Rothschild, L. J., M. A. Ragan, A. W. Coleman, P. Heywood, and S. A. Gerbi. 1986. Are rRNA sequence comparisons the Rosetta Stone of phylogenetics?—Cell 47: 640.

Saint Laurent, M. de, and R. Cleva. 1981. Crustacés décapodes: Stenopodidea.—*In:* Résultats des Campagnes MUSORSTOM I. Philippines (18–28 Mars 1976), 1(7), Memoirs ORSTOM 91: 151–188.

Sankoff, D., C. Morel, and R. J. Cedergren. 1973. Evolution of 5S RNA and the non-randomness of base replacement.—Nature New Biology 245: 232–234.

Schram, F. R. 1984. Relationships within eumalacostracan Crustacea.—Transactions of the San Diego Society of Natural History 20: 301–312.

———. 1986. Crustacea.—Oxford University Press, New York, New York, and London, England Pp. 1–606.

Spears, T., and L. G. Abele. 1988. Molecular phylogeny of brachyuran crustaceans based on 18S rRNA nucleotide sequences.—American Zoologist 28(4): 2A. [Abstract.]

Swofford, D. L. 1985. PAUP, Phylogenetic Analysis Using Parsimony, user's manual version 2.4.—Illinois Natural History Survey, Champaign, Illinois.

von Heijne, G. 1988. Getting sense out of sequence data.—Nature 333: 605–607.

Woese, C. R. 1987. Macroevolution in the microscopic world.—*In:* C. Patterson, ed., Molecules and morphology in evolution: conflict or compromise? Pp. 177–202. Cambridge University Press, London, England.

RECEIVED: 24 July 1989.
ACCEPTED: 3 October 1989.

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Appendix 1. Nucleotide sequences of 18S rRNA for the taxa studied. N = unknown, · = alignment gap, 1 = *Procambarus leonensis*, 2 = *Callinectes sapidus*, 3 = *Stenopus hispidus*, 4 = *Palaemonetes kadiakensis*, 5 = *Procaris ascensionis*, 6 = *Penaeus aztecus*, 7 = *Artemia salina*.

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1.  NNCCUGGUUGAUCCUGCCAGNAGUCAUNNGCUUGUCUCAAANAUUAAGCCNNGCAUGUGUAAGUACAAGCCGAGUUAAGGCGAAACCGCGAAUGGCNCNNNUAAAUCAGCUA
2.  NNCCUGGUNGAUCCUGCCAGNAGUCNUNNGCUUGUCUCAAANNUUAAGCCNNGCAUGUCUNAGUACAAGCCGAAUNAAGGCGAAACCGCGAAUGGCUNNNNUAAAUCAGCUA
3.  NNCCUGGUNGAUCCUGCCAGNNGUCNUNNGCUUGUCUCAAANNUUNAGCCNNGCAUGUGUGAGUACAAGCCCAAGGAAGGUGAAACCGCGAAUGGCNNNNUAAAUCAGCUA
4.  NNCCUGGUNGAUCCUGCCAGNAGUCNUNNGCUUGUCUCAAANNUUAAGCCANGCAUGUGUCAGUACAGGCCGCUCUAAGGCGAAACCGCGAAUGGCUNNNUAAAUCAGUUA
5.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNGCAUGUCUAAGCACAGGCCGAACUAAGGCUAAGCCGCGAAUGGCNNNNUAAAUCAGUUA
6.  NNCCUGGUNGAUCCUGCCAGNNGUCNUNNGCUUGUCUCAAAGAUUAAGCCNNGCAUGUGUAAGUACAGGCCGACNNAAGGCGAAACCGCGGACGGCNNNNUAAAUCAGAUA
7.  UACCUGGUUGAUCCUGCCAGUAG.CAUAUGCUUGUCUCAAAGAUUAAGCCAUGCAUGUCUAAGUACAAGCCCCCAGUGGGCGAAACCGCGAAUGGCUCAAUAAAUCAGUUA

1.  UGUUUCAUUGGAUCUGU....AAACNNNCNNNNACUUGGAUAACUGUGGUAAUUCUAGAGCUN.AUACAUG.CAUCAC..GUCUCUGAC.CGCAAG..GGAAGAGCGCUUU
2.  UGAUUCAUUNNAUCUGU......ACCCNCNCNNACUUGGAUAACUGUGGUAAUUCUAGAGCUA.AUACAUG.CAUUAC..GUCUCUGAC.CGCAAG..GGAAGAGNGCUUU
3.  UGGUUUACUGGACCUGU....ACUNCNNUNNNNNNNNNNNNNNNNNNNGGUAAUUCUAGAGCUN.ANNCNNG.CCNCGA..G.CNCNGACGCGGGAGCGGGAAGAGCGCNNN
4.  UCAUUCAUUUNAUCUAA....AACNNNNNNNNNNNNNGGNNAANNNNGGUAAUUCUAGAGCUNNANACGUGACUUGUN..AACNCCGAC.NGGAAG..GGAGGAGNGCUUN
5.  UGGUUCAUUNNNNNNNN....NNNNNNNNNNNNNNNNNNNNNNNNNGGUAAUUCUAGAGCUN.NNNNNNN.NACCCA..CGCUCCGAC.CGCGAG..GGAGGAGNGCUUU
6.  UAACUCAUUNNAUCUCUGCUGAACNNCNUNNNNNNUUGGAUAACUGUGGUAAUUCUAGAGCUN.N.ACAUG.CCUUUGUANNCUCCGAC.CGCGAG..GGAGGAGNGCUUU
7.  UGGUUCCUUAGAUC.GU......ACUAUAUCCUACUUGGAUAACUGUGGUAAUUCUAGAGCUA.AUACAUG.CACAAU..AGCCCCAAC.UUCACG..GAAGGGGUGCUUU

1.  UAUUAGUUCAAAA...C..........UGGUCGG.......GCCU.CGGUCCGUUNA......CC.CACC.CGUGGUGAAUCUGAAUAACUUUUUGCUGAGCGCACGGNC
2.  UAUUAGUUCAAAA...C..........CGGUCGG.......GCCU.CGGUCCGNNNC......CC.CACU..GUGUUGAAUCUGAAUAACUUUUUGCUGAGCGCACGGUC
3.  .ANNAGUACNAAAACCN..........GNGUCUGUGUAUCGGCUU.AGGUCGUUGCAUAGNCNNN.NNNN.UGUGGUGACUCUGAAUAACUUUUGGCUGAGCGCAUGGUC
4.  UAUUAGUUGAAAA...C..........CAAGCGG.......GCCN.CGGUCCGNNNN......NN.NNNC.UGUGAUGACUCUGAAUNACUUUGUGCAGAGAGCACGGNC
5.  UAUUAGUUGAAAA...C..........CAACCGG.......GCCN.CGGUCCGCNAA......AGACANC.UGUGGUGAAGCUGAAUAACUUUGUGCCGAGCGCACNGNC
6.  UAUUAGACCAAAA...CCCUCGGCAGCNNNNUCCC.......GCAA.GGGNCNAGCAG......CA.CACAUCUUGGUGAAUCAGAAUAACUUUUGCCGAGGCACGACCCC
7.  UAUUAGAUCAAGA...C..........CAAUCGG.......GGCUUCGGCUCGU.............CU.CUUGGUGACUCUGAAUAACUAUA.GCCGAUCGCACGGUC

1.  UCCGCA............CC.GGCGCCGCAUCCUUCAAGUGUCUGCCUUAUCA.G.CUUUCGAUUGUAGGUUAUGCGCCUACAAUGGCUAUAACGGGUAACGGGGAAUCAG
2.  UCNGCN............C...GCGCNGCCUCUUUCAAGUGUCUGCCUUAUCA.G.CUUUCGAUUGUAGGUUAUACGCCUACNAUGGCUNUNACGGGUAACGGGGAAUGAG
3.  UCCGCA............CCUGGCGCCGCAUCUUUCAAGUGUCUGCCUUAUCA.G.CUGUCGAUUGUAGGUUAUGCGCCUNNNAUGGCGAUNNCGGGUAACGGGGAAUCNG
4.  UNNGCA............CC.GGCUCCGUAUCUUUCGAGUUUCUGCCUUAUCAUG.CUGUGGAUUGUAGGCCAUGCGCCUNCNGUNGCUGUUNCGGGUAACGGGGAAUCAG
5.  NNNNCA............CC.GGCGCCGAUUCCUUCGAGUGUCUCGCUUAUCA.GGCNGUCGAUUGUAGGUUAUGUGCCNNNNNNNNNNNNNNCGGGUAACGGGGAAUNNN
6.  UCCGUAACNNGGGNUGGGNC.GGCGCCGCGUCCUGCAGGCGUCUGCCUUAUCA.G.CUCUCGAUUGUAGGUUAAACGCCUACAAUGGCUAUNNCGGGUAACGGGGAAUNNN
7.  UC.GCA............CC.GGCGACGUGUCUUUCAAAUGUCUGCCUUAUCA.A.CUUUCGAUGGUAGGCUAUGCGCCUACCAUGGUUGCAACGGGUAACGGGGAAUCGG
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1.  GNUUCNAUUCCGGAGAGGGAGCCUGAGAAACGGCUACCACAUCUAAGGCA.....GGCAGCAGGCACGCNNAUUACCCACUCCCGGCACGGGGAGGUAGUGACNAAAA
2.  GGUUCGAUUCCGGAGAGNGAGCCUGAGAAACGGCUACCACNUCUNAGGNN.....GGCAGCAGGCACGCNNAUUACCCACUCC.GGCNCGGGGAGGUAGUGACNAAAA
3.  GGUUNNNUUCCGGAGANNGNGCCUGAGNNNCGGCUNCCNNNUNUNNNNNNNNNNNNNNGGCNGNAGGCNNNNNNAUUACCCN.UUCCGGCNCGGGGAGGUAGUGACNAAAA
4.  GNNUCGAUUCCGGAGAGGGAGCCUGAGNAACGGCUACCACAUCCAAGGNN.....GGCAGCAGGCACNNNNAUUACCCAAUCCCAGCUCUGGGAGGUAGUGACNAAAA
5.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNGGCAGCAGGCANNNNNAUUACCCACUCCCGGCUUGGGGAGGUAGUGACNAAAA
6.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNGGCAGCANGCGCNNNNAUUACCCNCUC..GGCNCGGGGAGNNAGUGACNAAAA
7.  GGUUCGAUUCCGGAGAGGGAGCCUGAGAAACGGCUACCACAUCCAAGGAA.....GGCAGCAGGCGCGCAAAUUACCCACUCCCAGCACGGGGAGGUAGUGACGAAAA

1.  AUAACGAUGCGAGACUCAUCCGAGGCCUCGCAAUCGGAAUGAGUACACUUUAAANCCUUUAACGAGGAUCUAUUGGAGGGCNAGUCUGGUGCCAGCAGCCGCGGUAAUUCC
2.  AUAACGAUGCGAGACUCAUCCGNGGCCUCGNNAUCGGAAUGAGUNCACUUUAAAUCCUUUNACGAGGAUCUAUUGGAGGGCNAGUCUGGUGCCAGCAGCCGCGGUAAUUCC
3.  AUAACGAUGCGAGACUCAUCCGAGGCCUCGCNAUCGGAAUGAGAACACUUUAAAUCCUUUNUCGAGGAUCGAUUGGAGGGCAAGUCUNGUGCCAGCAGCCGCGGUAAUUCC
4.  AUAACAAUGCGGGACUCUUCCGAGUCUGCGUAAUUGGAAUGAGCACACUUUAAAUCCUUUAGCAACNACCNAUUGGAGGGCAAGUCUGGUGCCAGCAGCCGCGGUAAUUCN
5.  AUAACGAUGCGGGACUCAUCCGAGGCCNCGCAAUUGGAAUGAGUACACUUUAANUCCUUUAACGAGGACCCANNNNNNNNNNNNNNNNNNNNNCAGCAGCCGCGGUAANNNN
6.  AUACUGUUNGNNGACC...CCGNGNCCUCGCNAUUGGAAUGAGUNCACUUUAAAUCCUUGUACGAGGAUCGAGUGGAGGGCAANNNNNNNNNNCAGCAGCCGCGGUAAUUCC
7.  AUAACGAUGCAGGACUCAUCCGAGGCCCUGUGAUUGGAAUGAGUACACUUUAAAUCCUUUAACGAGGAUCCAUUGGAGGGCAAGUCUGGUGCCAGCAGCCGCGGUAACUCC

1.  AGCUCCAAUANNGUAUAUUAAAGUUGUUGCGGUUNN.AAAGCUCGUAGUUGGAUCUCAGUUCCGGACUGACGGUACA..CGCNNGGUGCUUACUGUCACGCUCCGAACAGC
2.  AGCUGCAAUANNGUAUAUUAAAGUUGUUGCGGUUANNAAAGCUCGUAGUUNNAUUUCAGUUCUGGACUGACGGUUNC..CGCNNGGUGCACACUGUCACNCUCCGAACAGC
3.  AGCUCCAAUAGNGUAUAUUAAAGUUGCUGCGGNUNN.AAAGCUCGUAGUUNNAUCUCAGUUC.GGACGGCCGNCNUC..CNNNGUGCNUUUUGCGGCUUGAUCCGAACA.C
4.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN.NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN..NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
5.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN.NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN..NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
6.  AGCUCCACUAGCGUAUAUUAAAGUUGUUGCGGUUGA.AACGCUCGUAGUUUGACUUCUGCUC.GGACGG.CGGN.......CUUNNCNGCUACUGCCGNNUUCCGAGCUG.
7.  AGCUCCAAUAGCGUAUAUUAAAGUUGCUGCGGUUAA.AAAGCUCGUAGUUGGAUAUGGGUCUCGGUCGGGUGGUGCCGCCUCACGGUGGUCACUGCCUCGAUC.GGACAAU

1.  UAACUAGCCCCGCCGGCCAGUGGGGUGCUCUUCAU......CGAGUGUCCCGAGUGGCCGGNNCGUUUACUUUGAACAAAUUAGAGUGCUCAGAGCNGGCNNCNNNNAUG.
2.  CA..CAACACCGCUGGCCNNNGGGGUGCUCUUCNC......CNGGUGUCCNNNNNNNNNNNNNNNNNNACUUUGAACAAAUUANNNNNNNNNNNNNNNNNNNNNNNNNNN.
3.  UN.CUGUUGUGGGCGCGCAG.GGGGUGCUCUUGAU......CGAGUGUGCNNNNNNNNNNNNNNNNNNNACUUUGAACAAAUUANNNNNNNNNNNNNNNNNNNNNNNNNNN.
4.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN......NNNNNNNNNNNNNNNNNNNNNNNNNNNNACUUUGAACAAAUUANNNNNNNNNNNNNNNNNNNNNNNNNNN.
5.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN......NNNNNNNNNNNNNNNNNNNNNNA.GUUUACUUUGAACAAAUUAGAGUGCUCAGAGCAGGCUAAUUNAAUG.
6.  UGUCCCCNGCCGGCGCACAUGGGGNUNNNNUGCCUUAANNNCGGGNGUCCCCUNNNNNNNNNNCCGUUACUUUGAACAAAUUAGAGNGCNNAGAGCAGGCNNGNNNNNNNN
7.  UCAUUGGAUCGUUCGG.......GGUGCUCUUAAC......CGAGUGUCCUGGGUGGCCGAUACGUUUACUUUGAACAAAUUAGAGUGCUUAAAGCAGGUGCACCGC....

1.  ....GCCUGA.AUGUCUAUGCACUGGAAUAAUGGAAUAG.GACCUCGGUUCUAUUUUGUUGGUUUU.C...GGAACCUGAGGUAAUGACUAAUAGGAACAGGCGGGGGCAU
2.  ....NCCUGA.AUGCCUAUGCANUGGAAUAAUGGAAUAG.GACCUCGGNNCUNUUUUGUCGGUUUU.C...UGAACCCGAGGUAAUGACUAAUAGGAACNGGCGGGGGCNU
3.  ....CCCUGA.AUGACUUUGCA.UGGAAUAAUGGAAUAG.GACCUCGGUUCUAUUUUGCUGGUUUU.GUCUGGAACCCGAGGUAAUGACUAAUAGAAACNGGCGGGGGNNU
4.  ....NNNNNA.UGUNCCUUGCAUGGAACUGAUGGAAGACUGAUCUCGGUUCCACNUUCUUGGUGGU.G...GGAGCCAGAGGUAAUGAUCNAGAGGGNCUGUCNNNNNNNU
5.  ....GCCCGCUAUGUUUCCUGCAUGGAAUGAUGGAAGAU.GACCUCGGUUCCAUUUUGUUUGUUUU.C...GGAACCCGAGGNNAUGAUGAAUAGAGACGGACGGGGGCAU
6.  NNCAGCCCGA.AUGGUCGUGCA.UGGAAUGAUGGAACAG.GACCUCGGNUCUAUUUUGUCGGUUUUUC...GGAACCCGAGGNNAUGAUUNAUAGAAGCAGACGGGGGNNU
7.  ....GCCUGA.AUAUCACAGCA.UGGAA[U]GAUGGAAUAG.GACCUCGGUCUUAUUAUGUUGGUUUU.C...UGGACUUGAGGUAAUGGUUAACAGAGACAGACGGGGGCAU
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1.  UCGUAUUGCGACGCUAGAGGUGAAAUUCUUGGACCGUCGCNAGACGAACUACUGCGAAAGCAUUUGCCAAGGAUGUUUUCAUUAAUCAAGAANGAAAGUUAGAGGUUCGAA
2.  UCGUAUUGCGACGCUAGAGGUGAAAUUCUUGGACCGUCGCNAGACGAACUNCUGCGAAAGCAUUUGCCNAGGAUGUUU.CNUUNAUCNAGAANGAAAGUUAGAGGUUCGAA
3.  UCGUACUGCGACGCUAGAGGUGAAAUUCUUGGACCGUCGCNAGACGAACUNAUGCGAAAGCAUCUGCCNAGGAUGUUUUCNUUNAUCNAGAANGAAAGUUAGAGGUUCGAA
4.  CCGUACUACGACGCGAGAGGUGAAAUUCUUGGACCGUCGUAGGACGAACCACAGCGAAAGCAUUUGCCNAGAAUGUCUUCGUUGAUCNAGAANGAAAGUUAGAGGAUCGAA
5.  CCGNNCUGCGACGUGAGAGGUGAAAUUCUUGGAAUGUCGNNAGACGAACGACAGCGAAAGCAUUUGCCAAGUAUGUCUUCGUUAAUCAAGAANGAAAGUUAGAGGUUCGAA
6.  UCGUACUGCGACGCUAGAGGUGAAAUUCUUGGACCGUCGCAUGACGACCUNCUGCGAAAGCAUCUGCCNAGGAUGUUUUCAUUGAUCAAGAANGAAAGUUAGAGGUUCGAA
7.  UCGUACUGCGACGCUAGAGGUGAAAUUCUUGGACCGUCGCAAGACGAACAACUGCGAACAAGUUUGCCAAGAAUGUUUUCAUUAAUCAAGAACGAAAGUUAGAGGUUCGAA

1.  GGCGAUCAGAUACCGCNCNNGUUNNAACCAUAAACGAUGCCAACUAGCGAUCCGCCGGCGUUAUUCCCAUGACCCGGCNGNCAGCU..UCCGGGAAACCA.AAGUCUUUGG
2.  GGCGAUCAGAUACCGCNNNNNNNNNAACCAUAAACGAUGCUGACCAGCGAUCCGCCGGNNUUAUUNNCAUGACCCGGCCNCCAGCU..UCCGGGAAACCA.AAGUCUUUGG
3.  GGCGAUCAGAUACNNNNNNNGUUCUAACCAUAAACGAUGCUNACCAGCNAUCCGCCCGCGUUNUUCCCAUGACCGGGCNNNNNGCU..UCGGGGAAACCA.AAGUCUUUGA
4.  GGCGAUCAGAUACNNNNNANGAAAGAACCAUAAACGAUGCUGACUNGCAAUUCGCNGNNGUUNUUCCCAUGACGUGCGAGAC.GCC..CCCGGGAAACCUCAAGUCUUUGA
5.  GGCGAUCAGAUACCGCCCNNGUUCUAACCAUAAACGAUGCUGACCAGCGAUCCGCCGGCGUUAUUCCCAUGACGCGGCGGNNAGCUACUCCGGGAAACCA.AAGUCNNUGA
6.  GGCGAUCAGAUACNGCNCNNGUUCUAACCAUAAACGAUGCUGACUAGCGAUCCGCCGCAGUUAUUNNCAUGACCCGGCGNNNAGCU..UCCGGGAAACCA.AAGUCUUUGG
7.  GGCGAUCAGAUACCGCCCUAGUUCUAACCAUAAACGAUGCCAACCAGCGAUCCGCGGACGUUACUUGAAUGACUCCGCGGGCAGCU..UCCGGGAAACCA.AAGUGUUUGG

1.  GUUCCGGGGGAAGUAUGGUUGCAAAGCUGAAACUUAAAGGAAUUGACGGNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNAACACGGGGAACCUCACCAG
2.  GUUCCGGGGGAAGUAUGGUUGCAAAGCUGAAACUUAAAGGAAUUGACGGNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNACACGGGGAACCUCACCAG
3.  GUUCCGGGGGAAGUAUGGUUGCAAANNNGAAACUUAAAGGAAUUGACGGNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
4.  GUUCCGGGGGAAGUAUGGUUGCAAAACUGAAACUUAAAGGAAUUGACGGNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNAACACGGGAAACCUCACCAG
5.  GUUCCGGGGGUANNNNNNNNNNNNNNNNNAAACUUAAAGGAAUUGACGGNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
6.  GUUCCGGGGGAAGUAUGGUUGCAAAGCUGAAACUUAAAGGAAUUGACGGNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
7.  GUUCCGGGGGAAGUAUGGUUGCAAAGCUGAAACUUAAAGGAAUUGACGGAAGGGCACCACCAGGAGUGGAGCCUGCGGCUUAAUUUGACUCAACACGGGAAACCUCACCAG

1.  GCCCAGACACCGGAAGGAUNGACAGAUUGAGAGCUCUUUCUCGAUUCGGUGGGUGGUNGUGCAUGGC...CGUUCUUAGUUGGUGGAGCGAU.UUGUCUGGUUAAUUCCGA
2.  GCCCAGACACCGGAAGGANNGACAGAUUGAGAGCUCNNUCUC.AUUNGGUGGGUGGUNGUGCAUNNCG..NGUUCUUAGUUGGUGGAGCGNN.NNNNNNNNNNNNNNNCGA
3.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNUGCAUGG..UNNN...NNNNNNNNNNNGGUGGAGCGAU.UG..CUGGUUAAUUCCGA
4.  GCCCGGACACCAGAAGGANNGACAGAUNNAGAGCUCUUUCUCGAUUUGGUGGGUNNNNNUGCAUGGC...NGUUCUUAGUUGGUGGAGUGAN.NNNNNNNNNNN....CGA
5.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNUGCAUNNN...NGUUCUUAGUUGGUGGAGCGAU.UUGUCUGGUUAAUUCCGA
6.  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNGU...GCAUGGGUCGNGUUCUUAGUUGGUGGAGUGAUCNNNNNNNNNNNNNNNCGA
7.  GCCCGGACACUGGAAGGAUUGACAGAUUGAGAGCUCUUUCUUGAUUCAGUGGGUGGUGGUGCAUGGC...CGUUCUUAGUUGGUGGAGCGAU.UUGUCUGGUUAAUUCCGA

1.  UNNNNNNNGAGACUCUGGCCUAUUAACUAGUCGACGGAUCUCCAGCNNUUG.GUGUCCAGUUCGCAA.CU.UCUUCUUAGAGGGAUUA.CGGCA.........AUUCUAGC
2.  UNACGAACGAGANNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNGUGUCCAGUUCGCAG.CU.UCUUCUUAGAGGGAUAA.CGGCA.........AUUCUAGC
3.  UNACGAACGAGACUCGGACCUACUAACUAGUCGACGGAUCUUCGUCCGACG.GUGUCCAGUUCGUNA.AG.UCUUCUUAGAGGGAUAA.CGGCA.........AGUGUAGC
4.  UNACGAACGAGANNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN.NCC.CCNGUUCGANN.NNGUCUUCUUNGAGGGAUGAGCNGCG.........AGUNUAGC
5.  UAACGAANGAGACUNUGGCCUACUAACUAGUCGACGGGUCUCCAGCNNUUG.GUGCCCAGUUCGCAA.CA.UCUUCUUAGAGGGAUAAGCGGCA.........AUUCUAGC
6.  UNACGAACGAGANNNNNNNNNNNNNNNNNNNNNNNNNGGCGCCGGNAACNG.GCGNUC..NUCGCNGUCU.UCUUCUUAGAGGGAUAAGCGGCAGCNAAAAUAUACUAGC
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1.  CGCACGAGA..UUGAGCAAUAACAGGUCUGUGAUGCCCUUAGAUGUUCUGGGC.GCACGCGCGCUACACUGAAGAGAUCAACGUGUUC.UCCCCCUCCGAGAGGACCGGGN
2.  CGCACGAGA..UUGAGCAAUAACAAGUCUGUGAUGCCCUUAGAUGUUCUGGGC.GCACGCGCGCUACACUGAAGGGAUCAACGUGUCC.UCCCNCUCCGAGAGGACCGGGN
3.  CGCAGGAGA..UCGAGCAAUAACANGUCUGUGAUGCCCUUAGAUGUUCUGGGC.GCACGCGCGCUACACUGAAGUGUUCAACGUGUUG.UCCCNGUCCGAGAGGACCGGGN
4.  UGCAGGAGA..UUGAGCAAUAACANGUCUGUGAUGCCCUUAGAUGUCCUGGGC.GCACGCGCGCUACACUGAAUGGGUUAGCGGGUUG.UCCUUCUCCGAGAGGACCGGGN
5.  CGCACGAGA..UUGAGCAAUAACAAGUCUGUGAUGCCCUUAGAUGUCCUGGGC.NCACGCGCGCUACACUGAAGGGGGCAGCGGGNNU...CCNCUCCGAGAGGACCGGGN
6.  CGCACGAGAGUUUGAGCCAUAACANGUCUGUGAUGCCCUUAGAUGUUCUGGGC.GCACGCGCGCUACAAUGGAGAGUUCAGCGAGCUNGNCCCNCUCCGAGAGGACCGGGN
7.  CAUAUGAGA..GUGAGCAAUAACAGGUCUGUGAUGCCCUUAGAUGUCCUGGGCCGCACGCGCGCUACACUGGAAGAAUCAGCGCGUCC.UCCCUGUCCGAGAGGACCGGGU

1.  AACCCGUUCAAUCCCCUUCAUGAUAGGGAUUGGGGCUUGCAAUUGUUUCCC.AUGAACGAGGAAUUCCCAGUAAGUGCAAGUCAUCACGUUGCGCUGAUUNNGUCCCUGCC
2.  NNCCCGUUGAAAUCCNUUCAUGAUAGGGAUUGGGGUUUGCAAUUGUCUCCC.AUGAANNNGGAAUUCCCAGUAAGCGCAAGUCAUGAGCUUGCGNUGAUUNNGUCCCUNCC
3.  NNCCCGCUGAAAGCNUUUCUUGAUNGGGAUGGGGGCUUGCAAUUGUUCCCN.NUGAANNNGGAAUUCCCAGUAAGCGCAAGUCAAUAGCUUGCGNUGAUNNNGUCCCUNCN
4.  NAUCGCGUGAAAACCAUUCGUGAUNGGGAUUGGGGCUUGCAAUUGUUUCCCNAUGAANGAGGAAUUCCCAGUAAGCGCAAGUCAUCAGCUUGCGNUGAUUNNGUCCCUNCC
5.  AACCNCUUGAAAACCUNUCAUGAUAGGGACUGGGGCNUGUAAUUGNUUCCC.AUGAACGAGGAANNCCCAGUAAGCGCAAGUGNNNNNNNUGCGCUGAUUNNGUCCCNNCC
6.  NCCUGCGUGAAAGCUGUCCUUAAAGGGGAUUGGGGCUUGCAAAUGUUCCCN.AUGANNNNGGAAUUCCCAGUA.GCGCAAUUCNCCAGAUUGCGCGGAUUUAGUCCCUACC
7.  AACC.GCUGAACCUCUUCCGUGGUUGGGAUUGGGGACUGCAAG.GAUCCCC.AUGAACCAGGAAUCCCUAGUAGGCGCAAGUCAUUAGCUUGCGUCGAUUACGUCCCUGCC

1.  CNUUGUACACACCGCCCGUCGCUACUACCGAUUGAAUGAUUUAGUGAGG.CUUC.GGACUGGCGCUCUUGGAU..GUUCUACCCCUCGCGUCUCGGCGCAAG.....GNNN
2.  NNUUGUACACACCGCCCGUCGCUACUACCGAUUGAAUGAUUUAGUGAGG.CUUC.GGACUGGCGCUCUUGGAU..GC.CGGNCCCGAGNGGUUCNNCGCCGG.....NNCN
3.  NNUUGUACACACCGCCCGUCGCUACUACCGAUUGAAUGAUUUAGUGAGG.CUUC.GGACUGGCGCCCU.GGGU..CUGAUGCANGUUG.GCCUUAGUGCCUU.....GUG.
4.  CNUUGUACACACCGCCCGUCGCUACUACCGAUUGAAUGAUU.AGUGAGG.CUUC.GGACUGGCGGUCCUGGACUGGGUCGGCGGGUCNCNCCCAGCNNUGGGNUUCCGCCN
5.  NNUUGUACACACCGCCCGUCGCUACUACCGAUUGAAUGAUUUAGUGAGG.CUUC.GGACUGGCGCUCCUNGA.....ACGACCCCAUCCGANNGGGNNCCCN.....GGNN
6.  CNUUGUACACACCGCCCGUCGCUACUACCGAUUGAAUGGUCUAGUGAGG.GNNCCGGACUNGCGCCCNUGGA...GCCCUACCCUCNGCGNCN..GCGC.............
7.  CUUUGUACACACCGCCCGUCGCUACUACCGAUUGAAUGAUUUAGUGAGAACUUC.GGAC..........GA......CUCGCCAGGGCAGCUCCGGGC.............

1.  UCUCGCCUCGAGCUGACGGAAAGAUGUCCAAACUUGAUNNNNNNNNNNNNNNNNNNAAGUCGUAACAAGGUNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
2.  CGGCGCCUCGAGCUGACGGAAAGAUGUCCAAACUUGAUNNNNNNNNNNNNNNNNNNAAGUCGUAACAAGGUNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
3.  UAUCGCCUAGGGNCGACGGAAAGAUGUCCAAACUUGAUNNNNNNNNNNNNNNNNNNAAGUCGUAACAAGGUNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
4.  NCUCGCCUGGACGGGCCGGAAAGAUGUCCAAACUUGAUNNNNNNNNNNNNNNNNNNAAGUCGUAACAAGGUNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
5.  ...CUCCUCGAGUCGACGGANNGAUGUCCAAACUUGANNNNNNNNNNNNNNNNNNAAGUCGUAACAAGGUNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
6.  .....CCUCGGGUCGACGGAAAGGUGUCCAAGCUGGGUNNNNNNNNNNNNNNNNNNAAGUCGUAACAAGGUNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
7.  .CGCUCGUGGUGUGGUUGAAAGGUUGUUCAAACUUGAUCCUUUAGAGGAAGUAAAAGUCGUAACAAGGUUUCCGUAGGUGAACCUGCGGAAGGAUCAUUA
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