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The interrelationships of Acanthomorph fishes: A total evidence approach using molecular and morphological data

E.O. Wiley[a,b,*], G. David Johnson[b], Walter Wheaton Dimmick[a]

[a]*Natural History Museum and Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045, USA*

[b]*Division of Fishes, National Museum of Natural History, Washington, DC 20560, USA*

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Abstract

DNA sequence and morphological data were analyzed for specimens of twenty-five species of acanthomorph fishes and two specimens representing the outgroups Aulopiformes and Myctophiformes. A 572 base-pair (bp) segment of the 12S ribosomal mitochondrial gene, 1112 bp from three regions of the 28S ribosomal nuclear gene, and 38 morphological transformation series were analyzed under the criterion of maximum parsimony. The total evidence analysis resulted in a set of four most parsimonious trees. Relationships common to all trees are largely congruent with the hypothesis articulated by Johnson and Patterson (1993. Bull. Mar. Sci. 52, 554–626).

Keywords: Phylogenetic analysis; Molecular systematics; Acanthomorpha; Ctenosquamata; Paracanthopterygii; Euacanthopterygii; Acanthopterygii; Smegmamorpha; Percomorpha

1. Introduction

The Acanthomorpha (Rosen, 1973), or so-called spiny-rayed fishes, are the crown group of the major radiation of extant fishes, the Teleostei. With about 300 families and over 14,000 species, they comprise the majority of living teleosts, exhibiting remarkable morphological and ecological diversity. In habitat, they range from

* Corresponding author. Tel.: +1-785-864-4540; fax: +1-785-864-5335.
E-mail address: ewiley@eagle.cc.ukans.edu (E.O. Wiley)

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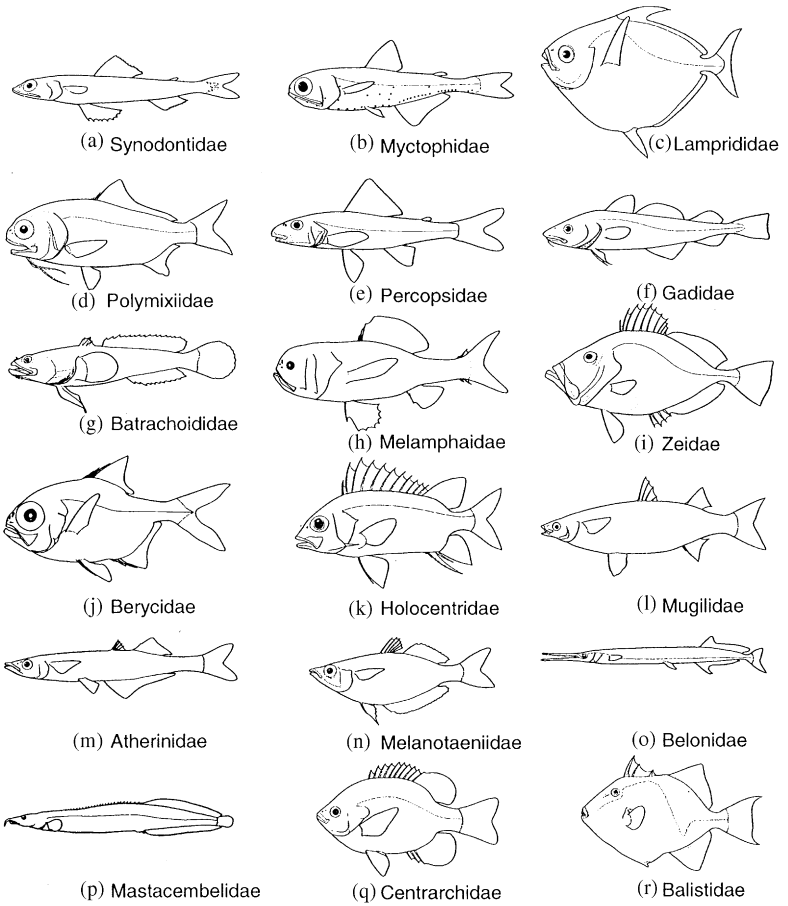

Fig. 1. Outline drawings of some fish groups used in this study: (a) Synodontidae, (b) Myctophidae, (c) Lamprididae, (d) Polymixiidae, (e) Percopsidae, (f) Gadidae, (g) Batrachoididae, (h) Melamphaidae, (i) Zeidae, (j) Berycidae, (k) Holocentridae, (l) Mugilidae, (m) Atherinidae, (n) Melanotaeniidae, (o) Belonidae, (p) Mastacembelidae, (q) Centrarchidae, (r) Balistidae. (Drawings from J. S. Nelson, 1994. Fishes of the World, Wiley-Interscience, New York. Used with permission.)

mountain streams to the abyssal depths of the ocean; some of their extensive diversity in form is evident in Fig. 1, where a representative of some of the families included in this study is shown in outline drawing.

The Acanthomorpha originated with Rosen's (1973) seminal paper on interrelationships of higher euteleosteans, and although the group found general acceptance (e.g., Fink and Weitzman, 1982; Lauder and Liem, 1983; Fink, 1984), there was considerable ambiguity in the distribution of the five characters used by Rosen to diagnose it. Rosen (1985) considered only two characters synapomorphic for acanthomorphs, and Stiassny (1986) presented four additional ones. Johnson and Patterson (1993)

considered new and previously proposed characters and accepted seven as providing valid support for monophyly of the Acanthomorpha. Rosen (1973) proposed that the Myctophiformes (lanternfishes and relatives) are the sister group of the Acanthomorpha and that the Aulopiformes (lizardfishes and relatives) are the sister group of these two together, a group he called the Ctenosquamata. Rosen (1985) challenged this hypothesis, but it was subsequently corroborated by Johnson (1992) and has not been challenged since.

Although the monophyly of the Acanthomorpha and its sister group relationships with other higher teleost groups (Neoteleostei) are now well established, the relationships among major lineages within the Acanthomorpha remain controversial. Johnson and Patterson (1993) reviewed, compared and evaluated the major alternative hypotheses (see their Figs. 2–4, 11, 18 and 19) and proposed a new hypothesis of acanthomorph relationships (their Figs. 24 and 25). The purpose of our study is to test the hypothesis of Johnson and Patterson (1993) using a combination of molecular and morphological data.

The morphological transformation series (i.e., characters) are those used by Johnson and Patterson (1993), and our strategy was to select taxa that would best allow us to test their hypothesis and pertinent alternatives. The final selection, however, was less than optimal, being constrained by the availability of tissue samples and the relatively small number of species that could be collected within the limited time frame of this study. As a consequence, our test of the Johnson and Patterson (1993) hypothesis is largely based on different acanthomorph taxa. The most notable differences are the following: (1) exclusion of the most basal family of Lampridiformes, Veliferidae, and substitution of *Lampris*; (2) inclusion of additional genera of Paracanthopterygii to test the monophyly of the group; (3) inclusion of the centrarchid *Lepomis macrochirus* to test the earlier hypothesis that *Elassoma* is most closely related to centrarchids among the families included in our study. In addition, we included genera of several major percomorph groups (e.g., Perciformes, Scorpaeniformes, Pleuronectiformes, Tetraodontiformes) in order to provide some representation of the extensive diversity within that assemblage. Although we mention some of the interesting ramifications of their inclusion in our analysis, we do not suggest that this is an attempt to explore percomorph intrarelationships. Such an investigation would obviously require much more comprehensive morphological data and wider and more extensive taxonomic coverage.

2. Materials and methods

Most specimens used for acquisition of DNA sequence data were collected in the field and immediately frozen in liquid nitrogen. Specimens used for morphological comparisons were taken from existing museum collections. Species examined are listed in Table 1.

Tissue samples were stored at $-70^{\circ}C$ until dissected. Approximately 0.1 g of tissue was dissected and DNA was extracted from frozen tissue by standard chloroform/phenol methods (Maniatis et al., 1982). We used the Polymerase Chain Reaction

Table 1
Species used in the present study

Aulopiformes (Synodontidae)
Synodus intermedius, SYN. USNM uncat. (Tissue No. 311).
Synodus variegatus. USNM 315318
Myctophiformes (Myctophidae)
Hygophum hygomii, HYG. KU uncat. (Tissue No. 263).
Hygophum macrochir. AMNH 25019
Lampridiformes (Lamprididae)
Lampris guttatus, LAM. USNM 357482, MCZ 255173, SIO 82-70.
Polymixiiformes (Polymixiidae)
Polymixia japonica, POL. KU uncat. (Tissue No. 258).
Polymixia lowei. USNM 308378.
Paracanthopterygii sensu Patterson and Rosen (1989)
Percopsiformes
Percopsis omiscomaycus (Percopsidae), PERC. UAIC 11218.07; USNM179711.
Aphredoderus sayanus (Aphredoderidae), APH. UAIC 10015.11; USNM217374.
Gadiformes
Pollachius virens (Gadidae), PLL. KU Uncat. (Tissue No. 359), USNM 187248.
Merluccius bilinearis (Merlucciidae), MER. KU Uncat. (Tissue No. 367), USNM 239843.
Batrachoidiformes
Opsanus tau (Batrachoididae), OPS. KU 22948, USNM 118326.
Ophidiiformes
Petrotyx sanguineus (Ophidiidae), PEX. USNM 327557.
Stephanoberyciformes
Scopeloberyx robustus (Melamphaidae), SB. KU uncat. (Tissue No. 276), USNM 215774.
Zeiformes
Zeus faber (Zeidae), ZEU. AMS NI1090; USNM 307842.
Zenopsis nebulosus (Zeidae), ZNP. AMS NI 1099
Zenopsis conchifer FMNH 67090.
Beryciformes sensu Johnson and Patterson (1996)
Beryx sp.(Berycidae), BER. KU uncat. (Tissue No. 827).
Beryx splendens. AMNH 95743
Holocentrus coruscus (Holocentridae), HOL. USNM 327564.
Holocentrus vexillaris. USNM 269553.
Percomorpha sensu Johnson and Patterson
Smegmamorpha sensu Johnson and Patterson (1996)
Elassomatidae
Elassoma evergladii (Elassomatidae), EL. UAIC 10854.02
Elassoma zonatum.USNM 230627
Atherinomorpha
Melanotaenia splendens (Melanotaeniidae), MEL. KU 25191.
Melanotaenia nigricans. USNM 173746.
Atherinomorus stipes (Atherinidae), ATH. USNM uncat. (Tissue No. 326).
Strongylura notata (Belonidae), STR. USNM 327560.
Strongylura marina USNM 292769.
Gambusia affinis (Poeciliidae), GAM. KU uncat. (Tissue No. 831).
Gambusia vittata. USNM 206285
Mugilidae
Mugil curema (Mugilidae), MUG. UAIC 10853.09.
Mugil cephalus USNM 156159

Table 1
Species used in the present study

Synbranchiformes	
Mastacembelus sp. (Mastacembelidae), MAS. KU 22982, AMNH 42129.	
"Higher" Percomorpha sensu Johnson and Patterson (1996)	
Perciformes	
Lepomis macrochirus (Centrarchidae), LEP. KU 25193.	
Lepomis marginatus. AMNH 79149.	
Morone chrysops (Moronidae). MOR. KU 22901.	
Morone americana. USNM 109851.	
Pleuronectiformes	
Bothus lunatus (Bothidae). BOT. USNM uncat. (Tissue No. 154).	
B. ocellatus. USNM 273281.	
Tetraodontiformes	
Melichthys niger (Balistidae). USNM uncat. (Tissue No. 105), ANSP 109442.	
Dactylopteriformes	
Dactylopterus volitans (Dactylopteridae). USNM uncat. (Tissue No. 237), USNM 348833.	

The structure of the classification uses a listing convention (Wiley, 1981) for the implied phylogenetic tree. Abbreviations are those used in the phylogenetic trees presented in Figs. 2 and 8. Both morphological and DNA data were collected for some species. First catalogue number refers to specimens from which DNA data were obtained. Second catalogue number(s) refer to specimens from which morphological data were obtained. When morphological data was collected on a close relative, the species is listed below and the catalogue number refers to a specimen for which morphological data were collected. Abbreviations follow, Leviton et al. (1985).

(Saiki, 1990) to amplify selected gene regions from genomic extractions. The 12S ribosomal mitochondrial gene region was amplified using amplitaq™ DNA polymerase from Perkin-Elmer Cetus corporation. Table 2 details the primers used in this study.

Amplified products were loaded onto NuSieve GTG® (FMC) agarose gels and electrophoresed at 85–90 V for approximately one hour. The target band was excised from the gel and the DNA was recovered with QIAquick™ gel extraction kits (Qiagen). The purified PCR product was manually sequenced with the fmol™ DNA sequencing system (Promega) using the primers indicated in Table 2.

Results were visualized by autoradiography and scored by visual inspection. Sequencing both strands was not accomplished in favor of maximizing our data for different regions and species. Two sources of error are possible, random and systematic. We presume that random errors such as misreading gels would lower signal and introduce spurious autapomorphies, but would not cause skewed results. We did encounter some systematic errors in the form of stops and compressions. We do not feel that these apparent artifacts have compromised our results because they usually effected all or most taxa when they occurred, and thus were easy to identify. Missing data values were used for ambiguous sites or for obvious compressions flanked by readable sequence. Finally, selected sequences were compared against results obtained using an automated sequencer (ABI 310 Genetic Analyzer) where complementry strands were sequenced. Only minor differences were observed in these sequences when compared to manual sequences and these were ascribed to errors in interpretation of the manual gels. All sequences were deposited in Genbank

Table 2
Sequencing (S) and amplification (A) primers used in this study

Name	Sequence	Strand	Use
Mitochondrial 12S gene			
12Sa[a]	5′AAACTGGGATTAGATACCCCACTA3′	Light	A, S
12Sb[a]	5′AGGAGGGTGACGGGCGGTGTGT3′	Heavy	A, S
12Sd[b]	5′GGGTTGGTAAATCTCGTGC3′	Light	A, S
Nuclear 28S gene			
28W[c]	5′CCTGTTGAGCTTGACTCTAGTCTG3′		A, S
28X[c]	5′GTGAATTCTGTTCACAATGATAGGAAGAGCC3′		A, S
28MM[d]	5′AGCCAATCCTTATCCCGAAGTTACG3′		A, S
28DD[c]	5′GTCTTGAAACACGGACCAAGGAGTCT3′		A
28EE[c]	5′ATCCGCTAAGGAGTGTGTAACAACTCACC3′		S
28FF[c]	5′GGTGAGTTGTTACACACTCCTTAGCGGAT3′		S

[a] Modified from Kocher et al. (1989).
[b] Modified 503 primer of John Patton, Washington University. Position in the human genome is 972–810.
[c] Hillis and Dixon (1991).
[d] Modified from Hillis and Dixon (1991).

(12S rDNA, AF149982–AF150008; 28ff rDNA, AF153285–AF153311; 28ee rDNA, AF150637–AF150663; 28mm rDNA, AF152115–AF152141; 28wx rDNA, AF152142–AF152168)

Initially, sequences were aligned by manual inspection. Next, we consulted secondary structure models of the 12S gene (Van der Peer et al., 1994) and the 28S rDNA gene for *Xenopus* (Clark et al., 1984) and produced heuristic models of the secondary structure of applicable regions for *Synodus*, one of our outgroup genera. This model was used to compare other species. Secondary structure, as indicated by complementry strands forming ladders flanked by unpaired loops, was then used to refine the initial alignments. The data were exported to MALIGN (Wheeler and Gladstein, 1994) using an option that constrains the data for alignment among presumed loop and stem regions. This alignment was inspected visually and adjusted for problematic alignments while maintaining the loops and stems of the secondary structure.

Stem and loop regions were examined for possible site saturation (multiple mutations at a site) by plotting the number of mutations between pairs of taxa against the Tamura-Nei genetic distance coefficients generated from MEGA 1.01 (Kumar et al., 1993). Thus, saturation studies were conducted on these classes of data separately. Gene regions composed of sites for which only ambiguous homology statements could be made due to the presence of gaps or saturation for all classes of substitutions were removed from the analysis, as presented in Section 3, Results. Classes of substitution that showed saturation were "screened" from the analysis using step-matrices, as presented in Section 3, Results. All remaining data were analyzed as unordered and equally weighted characters.

Data were collected for 38 morphological transformation series. Dissected cleared-and-stained specimens were examined using a Leitz dissecting microscope. Specimens

examined for morphological characters are different from those from which DNA data were obtained. The transformation series and associated characters listed below are modified from Johnson and Patterson (1993). One transformation series used by Johnson and Patterson (1993) was omitted ["extrascapular unmodified (0), or enlarged and covering parietal (1)"] because it is a synapomorphy for Stephanoberyciformes, a group represented by only a single species in the present study. Character numbers presented below correspond to column numbers in Fig. 2.

1685. — Dorsal and anal fins spines absent (0) or present (1).
1686. — Rostral cartilage absent (0) or present (1).
1687. — Medial caudal cartilages present (0) or absent (1).
1688. — Infracarinalis muscles joined (0) or separate (1).
1689. — Posttemporal loosely attached to epioccipital (0) or tightly attached (1).
1690. — Medial pelvic process ends in cartilage (0) or ends in bone (1).
1691. — First centrum unmodified anteriorly (0), or with exoccipital facets (1).
1692. — First epineural dorsolateral (0), or in horizontal septum (1), or absent (2).
1693. — Posterior pelvic process ends in cartilage (0), or ends in bone (1).
1694. — Spina occipitalis absent (0), or present (1).
1695. — Anterior (3–6) epineurals originate on neural arch (0), or on centrum, parapophysis, or rib (1), or are absent (2).
1696. — Epipleurals present (0), or absent (1).
1697. — Epicentral ligaments present on all or some of vertebrae 1–8 (0), or absent on these vertebrae (1).
1698. — Distal parts of epineurals 2–5 dorsolateral (0), in horizontal septum (1), or absent (2).
1699. — Pelvic fin spine absent (0), present with a symmetrical base (1), or present with a complex base (2).
1700. — Pelvic radials in a continuous row (0), or either in a discontinuous row or absent (1).
1701. — Anteromedial process of pelvic bone absent (0), or present (1).
1702. — Baudelot's ligament originates on first vertebra (0), on the basioccipital (1), on the exoccipital (2), or is absent (3).
1703. — Dorsal fin originates behind the fourth neural spine, supraneurals present (0), in front of the fourth neural spine, supraneurals present (1), in front of the fourth neural spine, supraneurals absent (2), behind the fourth neural spine, supraneurals absent (3), or anterior to the first neural spine, supraneurals absent (4).
1704. — Epineurals on vertebrae 3–6 on neural arch, centrum, or parapophysis (0), on rib (1), epineurals absent (2), or epineurals present but ribs absent (3).
1705. — Dorsal fin spines absent or without chain-link articulation (0), with chain-link articulation (1), or spine-bearing radials with no distal radials (2).
1706. — Supraneurals end distally in cartilage (0), in bone (1), or supraneurals absent (2).
1707. — Second ventral procurrent caudal ray unmodified or absent (0), or shortened proximally (1).

1708. — No ligament from shaft of postcleithrum to posterolateral corner of pelvic girdle (0), ligament present (1), or no ligament and girdle secondarily displaced posteriorly (2).
1709. — Uncinate process present on first epibranchial and interarcual cartilage absent (0), uncinate process present and interarcual cartilage present (1), uncinate process absent or not articulating with second pharyngobranchial and interarcual cartilage absent (2).
1710. — Second ural centrum distinct (0), or fused with first preural centrum + first ural centrum (PU1 + U1) (1).
1711. — Six hypurals (0), or five or fewer hypurals (1).
1712. — Pelvics with seven or more rays (0), or with six or fewer rays (1).
1713. — Transforming ctenoid scales absent (0), or present (1).
1714. — One or more free pelvic radials (0), or no free pelvic radials (1).
1715. — All or some epineurals above horizontal septum (0), all in horizontal septum (1), or two or fewer epineurals (2).
1716. — Principal caudal fin rays 19 (0), 18 (1), or 17 or fewer (2).
1717. — Distal and proximal ceratohyals separated by cartilage (0), sutured (1), or sutured with a dorsal prong (2).
1718. — Orbitosphenoid present (0) or absent (1).
1719. — Pelvic bones loosely attached or overlapping medially (0), with broad median contact (1), or sutured (2).
1720. — First epineural on neural arch or absent (0), or on transverse process (1).
1721. — Jakubowski's organ absent (0), or present (1).
1722. — Parahypural articulating with first preural centrum (0), or truncated proximally (1)

Morphological and DNA data were combined to form a total evidence matrix. Morphological data were analyzed as unordered and equally weighted characters.

Data analysis was carried out under the principle of maximum parsimony using PAUP 3.1.1 (Swofford, 1993) and PAUP*4.0d64. First, we performed a total evidence analysis in order to generate a phylogenetic hypothesis of relationship. This was carried out using a heuristic search with 20 random starting trees in an effort to avoid local parsimony optima (Maddison, 1991). Second, we performed three additional series of analyses using the same options, one each including the 12S rDNA and 28S rDNA data respectively and another including only morphological data.

We used three criteria to evaluate tree support for our total evidence analysis. First, we examined the support associated with each node. Three classes of transformation series were identified based on the consistency index: unique and unreversed (ci = 1.0), intermediate ($0.5 < ci < 1.0$), and low ($ci < 0.5$). Second, we performed a branch support analysis (Bremer, 1994) using the strict consensus tree that resulted from the total evidence analysis to check the robustness of the internal nodes that were common to each of the most parsimonious trees using the program Treerot (Sorenson, 1996). Third, we performed bootstrap analyses (Felsenstein, 1985) using the bootstrap option of PAUP using 100 replicates.

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                10        20        30        40        50        60        70
                 .         .         .         .         .         .         .

SYN     GGCGTAAAGG GTGGTTAAGA CAAAACCGTT --------CT AGAGGAAAAC ACCTTTCAA- ACTGTTATAC
HYG     .........C .........G GCTCCT.C-- ......AA.. .A..C.G... TG.C.C.GG. G.........
LAM     .........A .........C AG----..CCC CCCCT.AA.. .A..CC.... G..CCCA... G.C.......
POL     .........C .........G TT--.-ATA. .....AAA.. ....CCG... ...A.CA... G.........
PERC    ........A. ....C..G.G -T--.-AT.. T....ATA-. ..G.CCG... C..C.CT.G. G.........
APH     .....T...C ...A.....G TTT-..AT.- ......AA.. ....CC.... CA...CT... G.C.......
PLL     .........C .......... A..T.AGAGG .....AAA-. .CG.CCG... .A...CA... G.A.......
MER     .........C ........A. G..T..TAA- .....AAA.. ..G.CCG..T .G.C.CA... G.A.......
PEX     .........C .......G.. G..T.GAT.- .....AAA.. GAG.CT...T ..T...A... G.........
OPS     ...AC..... ........T. AT.---AT.- .....AAA-. .A..TC.... .TA...AC.. GT...-..CA
SB      ?..?.....A .........G ACT.-AT-.- .....AAA.. .A..CCG... G..C.CA... G.........
ZEU     .........C .........T A----..CCC CCCCCCAA.. ..G.CC.... ...CACG... G.........
ZNP     .........C .......G.C A----TACCC CCCC..AA.. ..G.CC.... ...C.CA... G.C.......
BER     .........A .......GAG A.C....C-- .....AAA.. .A..CCG... G....CA.G. G.........
HOL     .........A .......G.G A...CA.ACC .....AAA.. .A..CC.... .....CAG.. .........
MAS     .........A .......... AC.TT.TA-- .....AAA-. .A..TCG..T G.T..CT... G....C....
MEL     ...A.....C .......G.. G..TTTT--- .....AAA.. .A..CC.... ..TC.CAG.. .........
MUG     .........A .........T GT.TCTT.A. A....GAA.. .A..CCG... G..C.CA.G. ..C..C....
EL      .......... .........G A..GTTA--- .....AAA.. .A..CCG..T ..TA.CA.G. G.........
ATH     .........A .......... A...TTAT.- .....AAA.. .A..CCG... ..TC.CA... .........
STR     .........A .........G A...CT-T.- .....AAA.. .A..CCG..T .TT..CATG. G.........
GAM     .........C ........A. G---T..CAC T....AAA.. .AGACT.... CTT.CCA.G. G.........
LEP     .........A .........G G.G.T.A--- .....AAA.. .A..CCG..T G.T..CA... G.........
MOR     .........C .........G GCC...TT.. C....TA.. .A..CCG... G.T...AG.. G.A.......
DAC     .........T .........G A..CT..TC- .....AAA.. .A..CCG..T GT...CAC.. G.A..C....
MLI     .........A .......G.. A..C.TAAC- .....AAAT. .AG.CCG... G..C.CA.G. G.........
BOT     .......... .......G.G AG.C..ATC- ......AA.. .A..CCG..G G..G.CA.G. G.C..G....


                80        90       100       110       120       130       140
                 .         .         .         .         .         .         .

SYN     -GCA--CCCA AAGGTAAGAA AAACTTG-CA CGAAAGTCCC TCTAATAAA- --TCC-GAA- TCCACGACAG
HYG     ...-.T...G .C........ .CC.CA-C.. .......GG. .T...CCCGA ..C....... C......A..
LAM     .....CT..G ....GC...G G.CTCC-C.. ....G..GG. .T...ACC.. ..G.T..... C......A.C
POL     .........G .TA...T... G.T.CA-C.. ....G..GG. .....CC.CA CCC.T..... .......A..
PERC    ......T..G ....A.T... GC..CAA... .......AG. C...C-CT-. CCC....... C......A..
APH     ....A.T.-G ...AA.T... GCC..A-T.. .......AG. ....CA-T.. .CC.T..... C.....GA.A
PLL     ......T..G ...TC.C... G..-CAAT.. .......TG. C....A.T-. .C.......T .......A..
MER     .......T.G .GACC.C... GT..-AATT. .......AG. ....CCC--T AC.TT...-C .......A.A
PEX     .....TAT-G ..A.ATC... GC...A-CT. .......GG. CT..TA-C-. A...T....C -......A..
OPS     A...AAAT-. .TATAT-... GCC-CAAT.C ......AAA. .T..T--T-. AC.TT...-C A.....TA.A
SB      .......T.G .G....C... GCC.CA-T.. .......GG. .T...CCCCC A.C.T..... C......A..
ZEU     .....TGTTG .G.A.TT... GC..CC-C.. .A.....GG. C....ACCCC C.A.T...-. C......A..
ZNP     .......ATG .G.ACTT... G.T..C-CT. .A.....GG. C....ACCCT ..A.T..... C......A..
BER     ......T..G .....C.... G..ACCAT.. .......GG. .T..CCCCCC A.C....... C......A..
HOL     ..T......G ....C.T... G....A-C.. .......GG. .T..CC--.. A.C..T.... C......A..
MAS     ........TG ..A....... GCC.GAA... ....G..AA. .T..CA...T ....T...-C C......A..
MEL     ..T.....G .GAA.T...G GCC.C-CCT. .......GG. .T...CCC.T ....T...-C .......A..
MUG     ..TT..T..G .....T.... GCC-CAACT. .......AA. .T...-CTGT A........-C .......A..
EL      ...G.....G .TAA...... G.T-CAAC.. .......GG. .T..T---.T TCC.T..... C......A..
ATH     ..T......G .GA.C..... GTC-CCCC.. ......??G. .T....C-.T ....T....C C......A..
STR     ......T..G ..A....... GTT..A-CT. .......GG. .T....CT.. ..C.T...-C C......A..
GAM     .........G G.AA..T... .CT-CAACT. .......GG. CT....TT.C C.CTT...-C C......A..
LEP     ...-.TT..G ..A....... G.T-CAAT.. .......GG. .T..-CTTCC ..C.T...-C C......A..
MOR     ......-.TG .GA....... G.T-CAATT. .......AG. .T..-.TC.A A.C.T...-C C......A..
DAC     ...TA.-..G .......... GCC-CCTCA. .......GA. .T..TAT... ..C.T....C -......A..
MLI     ....C.-..G .GA....... GT.-CAACA. .......AG. C...TA..T. ....T....C -......A..
BOT     ...CCCTT.G .T..C.C... G.C-CAACT. .......GG. .T..C.T.G. ..C.T..-.C C....A.A..
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Fig. 2. *See p.* 339 *for caption.*

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                150        160        170        180        190        200        210
                 .          .          .          .          .          .          .

SYN     -CTCTGGTAC AAACTGGGAT TAGATACCCC ACTATGCTCA GCCGTAAACT TAGATGATCA A-TT-ATAAT
HYG     ...GG..A.. .......... .......... .......C.. .T.......A ..A..AGG.. .ACC..C..C
LAM     ...A.A.A.. .......... .......... ......TAT. ..TA...... .T...AGA.- CCC...C.-C
POL     ...A.AAA.. .......... .......... ......TAT. ...T.....C .T...AG--. .T.-..C.CA
PERC    ..CA.AAA.. .......... .......... ......TCTG ...C...... .C...AG--. .TA-.TC.CA
APH     T.CA.ATA.. .......... .......... ......TATG ..TA.....A A.....G.GT .TC-..C.CA
PLL     ..CA.AAA.. .......... .......... ......TATG .T...T...A .T....G.TT TA.-..CCCA
MER     ..CA.AAA.. .......... .......... ......TATG ..T..T...A .C..G.GC.C GA.-..CTCA
PEX     ...AA.AC.. .......... .......... ........T. ...A.....A C....A..GC CT.-..C..C
OPS     ...A.CTA.. .......... ....C..... ......T.T. .T........ ...-.AG--- -.--.-----
SB      ...AC.-A.. ..-..T..?. .......... ........-. ...C....AA .T...AG.A. TTC-ACCCCC
ZEU     ...A-----. .......... .......... ......TGT. .........C .T....G.A. CCC.C.CCCC
ZNP     ...ACAAA.. .......... .......... ......TGT. .........C .T....G.A. CC.GT.CCC.
BER     ...AC.TA.. .......... .......... .......CT. ...C.....A .....AG.A. CA.-..CTC.
HOL     ...A..TC.. .......... .......... ........T. ...A.....A .T...AGCGT TAC-..CCCC
MAS     ...AG.TC.. .......... .......... .......C.. ...T.....A ..A..AGCAC CCC-..C.T.
MEL     ...GA.AA.. .......... .......... .......... ...C...... .TA..AG.GC TA....--T.
MUG     ...G..AA.. .......... .......... .......C.. ...C...... .T...A..TT -A.C..C.C.
EL      ...A..A... .......... .......... ........T. ...C.....A .T....GGGT -AC...CCC.
ATH     ..CGG.AA.. .......... .......... .......C.. ...C...... .T...AGGAT .A....C.CC
STR     ...G..AA.. .......... .......... .......A.. ...C...... .T...AG..- .AG...C.CC
GAM     ...GC.AA.. .......... .......... .......A.. ...A...... .T...TGAA- .AC...C..A
LEP     ...A..AC.. .......... .......... .......CT. ...T.....A .C.GCA.CAC TT.-..C.CC
MOR     ...AA..C.. .......... .......... ........T. ...T.....A ....CAG.TG TT.-..CCCA
DAC     ...AG.AA.. .......... .C.GC..... .......CT. .........A A....AGAAT CC.-..C.CA
MLI     ...AA..C.. .......... .......... .......CT. ...T.....A .T...AGC.T .T.-..CTTA
BOT     CTGAA..A.. .......... .......... .......... ...C.....A .T...CGAAT TTA-..CTTA


                220        230        240        250        260        270        280
                 .          .          .          .          .          .          .

SYN     GT--TCATCC GCCAGGG-TA CTACGAGCGA AAGCTTAAAA CCCAAAGGAC TTGGCGGTGC TTCAGACCCC
HYG     AC..CT..T. ........G. ....A....T T.....C... .......... .......... ..T......A
LAM     ....CT.... ...C...GA. T........AC C......... .......... .........A. C.T...T...
POL     ACCCCT.... ...C....A. .........AC C......... .......... .......... ..T.......
PERC    CCC.CT.... .........A. ....A...AC C.....T... .......... .......... ..T.......
APH     A-..C...T. ...C....A. ....A...AC T......... .......... .......... ..T.T.....
PLL     AA..C..... ...T....G. .........A. T......... .......... .......... ..T.......
MER     .A..C.C... ...T..... .........AC T......... .......... .......... ..T.CC....
PEX     A-...T..T. .......... .........AT C......... .......... .......... ..T......A
OPS     --..----.. ......A... .........A. CT........ A......... C......... ..T.CT...-
SB      --..C?.... ...C..A... ....A....T ..........  .......... .......... ..T......A
ZEU     CCC.C..... ...T....A. .........AC C......... .......... .......... ..T.......
ZNP     T-..C..... ...T....A. .........C T......... .......... .......... ..T.......
BER     A-..CT.... ...C....A. .........AT T......... .......... .......... ..T......A
HOL     A-..CT.... ...C....A. .........A. T......... .......... .......... ..T...T..A
MAS     AG..CT..T. .........A. .........CT C......... .......... .......... ..T.A.T..A
MEL     .A..CT..T. ...T....A. ..........C T......... .......... .......... ..T...T...
MUG     CA...T.... ...T....A. .........TT C.....T... .......... .......... ..A...T..A
EL      CC..C..... ...T....A. .........AT .......... .......... .......... ..T...T..A
ATH     CC..CT.... ...C....A. .........AC T......... .......... .......... ..T...T...
STR     CA..CT.... ...C..... ....A...CC TT........ T......... .......... ..T...T..A
GAM     T...CT.... ...C....A. .........AT .......... .......... .......... ..T.......
LEP     CG..CTGC.. ......A.A. ..........T T......... .......... .......... ..T......A
MOR     CA..CTG... ...C..... .........AT T.....G... .......... .......... ..T......A
DAC     T-..CT.... ...C.AA... .........C .......... .T...G.... .......C.. ..T.T.A..A
MLI     AG..C..... ........A. .........AT T......... .......... .......... ..T...T..A
BOT     T...CT.... ...T....A. T....GA.AC T..TC..... A......... .......... ..T.C.T..A
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Fig. 2. *Continued.*

```
                290         300         310         320         330         340         350
                 .           .           .           .           .           .           ]

SYN     CCTAGAGGAG CCTGTTCTAG AACCGATATT CCTCGTTAAA CCTCACCGCC CCTTG-TTAG TC-CCGCCTA
HYG     .......... .....C.... ........AC ..C....C.. .......A.T T..C.CC... C-.......
LAM     .......... .......... ........C. ..C...CT.. .......A.. ...A.CCCCC CAA.......
POL     .......... .....C.... ........AC ..C....C.. .......A.. .........A AA........
PERC    .......... .........A ........A. ..C....G.. .......A.. TT.......A CT........
APH     .......... .........A ........AC ..C....T.. .......C.. TT......TA A.........
PLL     .......... .......... ...T....AC ..C....T.. .......AT. .T......TT C.........
MER     A......... .......... ...T....AC ..C....G.. .......AT. ...C....TA A.........
PEX     .......... .......... ........AC ..C....C.. .......C.. ........CC ..........
OPS     .......... ......TCTT ........A. ..C....CT. .......C.T T..C..C-.- ....A.....
SB      .......... .....C.... .......TCC ..C....C.. .......T.. ........T- ......T...
ZEU     .......... .......... ...T....AC ..C....... .......AG. .........A .A........
ZNP     .......... .......... ........AC ..C....C.. .......A.. .........A .A........
BER     .......... .....C.... ........AC ..C....C.. .......C.. .T......TT ..........
HOL     .T........ .......... ........A. ..C....C.. .......TTT ...A....TA A.........
MAS     .......... .........T ........AC ..C....C.. .......TT. .........A .T........
MEL     .......... .......... ........AC ..C....T.. .......C.. T.....C.CT .A.....T..
MUG     .......... .......... ........CC ..C....C.. .......CT. T.......TA ..........
EL      .......... .......... ........AC ..C....... .......CTT ...A..CCTT .T........
ATH     .......... .......... ........AC ..C....... .......CT. ........CC ..........
STR     .......... .....C.... ......C.AC ..C....... .......CT. .....T...T .TC.......
GAM     .......... .......... ........AC ..C..A..G. .......TTT T......CTA .T........
LEP     .......... .......... ........AC ..C....C.. .......CTT ........TT .TC.......
MOR     .......... .....C.... ........A. ..C....C.. .......CTT ...A..CCTT .AT.A.....
DAC     .-........ .......... .......TCC ..C....C.. .......CT. T.....C.TT .TT...T...
MLI     .......... .......... ........AC ..C....C.. .......TTT ........TT AT........
BOT     .......... ........GT ........AC ..C....... .......T.. ......CCTT AT...A....


                360         370         380         390         400         410         420
                 .           .           .           .           .           .           .

SYN     TATACCGCCG TCGTCAGCTT ACCCTTTGAA GGCGATTAAA GTAAGCAAGA --CAGTTAAA AA-CAAACAC
HYG     .......... .......... ....CG...G ...T..-.C. ......T.A. ..TT.GC.C. GCC....-..
LAM     .......... C.CC.....C ....CG...G ..ATTA-... .......... ...T.A..T. G-C....G..
POL     .......... .......... .....G.... ..AA..-.C. ........A. ..TT.G..T. .CC....-..
PERC    .......... C......... .....G.... ...CTC-.T. ........A. ..TT.GC.-. .CC.C..A..
APH     .......... .......... .....G.... ...CC--.T. ........A. ..TTAGC.C. GCC....-..
PLL     ......A... .......... .....G.... ..AA.A-.T. .......TA. ..AT.GC... GCCA...-..
MER     .......... .......... .....G.... ...C.A-.T. ........A. ..AT.GCT.. GCCA...-..
PEX     .......... ........C. .-...G.... ..ATTA-.T. ...G....A. ..TT.G..T. .CC....-..
OPS     .......... ..T....TC. .-.....C.. A.AATA-.T. T..G....A. TATCAACCTC CCCTC..A..
SB      ......A... .........G .....G.... ..TCTC..T. ........A. ..TT.A.... -TC...GA..
ZEU     .......... .......... .....G.... ...ATA-.T. ........AG ..TTAG.... .CT....-..
ZNP     .......... .......... .....G.... ..TTTA-.C. .......... ...TAG.... .CT....-..
BER     ......A... .......... .....G.... ...C-C..T. ........A. ..TT.G.... .CC....-..
HOL     .......... ...C...... .....G.... ..TC-C..T. ........A. A.TGA.CT.. .TC...G-..
MAS     .......... .......... ....CA.A.G ..TT.A-.C. .......TA. ..TT.G.TC. .CC.C..-..
MEL     .......... .......... .....G...G ..ACTA-.T. ..G.....A. ..TCAG..C. .CT....-..
MUG     .......... ........CC .....G.... ..TCCA-.T. ..G....G.. ..TC.G..G. .CC....-..
EL      ......A... .......T.. .....A.... ..ATTA-.C. .......... ...T.GC.CC ..C.T..A..
ATH     .......... .......... .....G.... ..ATTA-.T. ........AG ...CAGC.C. GCT....-..
STR     ........?. .......... .-...G.... .ATT.--.T. .......... ...CAGC.C. GCT....-..
GAM     .......... ........?? .-...G.... .ATA.--.T. ........A- ...T.G..-. .C......--.
LEP     ......A... .......... .....G.... ...CT.-.T. ........A. ..TT.GC.C. GCC..G.-..
MOR     .......... .......... .....A.... ..TAC.-... .......TA. ..TT.GC.CT GCCT...-..
DAC     .......... .......... .......... ..AC.A-.T. ..G.....A. ..TT.G.... .CC....-..
MLI     ......A... .......... .T...G.... ..TTTC-TT. A.......A. ..TT.GC... GCC....-..
BOT     .......... C......... .....GA..G .AG-.A-GTC ...T...GA. ..TT.GC.T. GCC....-..
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Fig. 2. *Continued.*

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                430         440         450         460         470         480         490
                 .           .           .           .           .           .           .

SYN     GTCAGGTCGA GGTGTAGCGG AGGGGGCGGG -AAGAAATGG GATACATTCT ATCATCC-AG AGAAAA--AC
HYG     .......... .........C .C.AA.T.T. C...TG.... .C.:....T. C.G.C..... .A..CT....
LAM     .......... .........C .T....T... ....C..... .C........ C.G.C....A .AT.T-....
POL     .......... .........T .T.A..T... .....G.... .C........ C.-.C.AC.. ..T.T-....
PERC    .......... .........T .T.A..T... .......... .C........ T...AA.C.. ....T-....
APH     .C........ .........C .TAA..G... .......... .C........ C...AT-.GA GATT.TT...
PLL     .......... .........A .T...AT... .......... .C........ C.ATCAT... ....T-....
MER     .......... .......T.A .T...AT... ......-... .C........ C.GT.A.... ....T-....
PEX     .......... .........T .C..A.G... ......-... .C......T. C.T.ATA... .A.---....
OPS     .......... ..C.....CA .T.AA.G..T ..CA...... .C.......C C...-.-... G.C.T-....
SB      .......... .........C .T.A..A... .....G.... .C........ C.AC.A.... .....-TA..
ZEU     .......... .........A .T.A.CT... .......... .C......T. C.-C.-TG.. .A...-....
ZNP     .......... .........A .T...TT... .......... .C......T. C.-C.-TG.. .AT.T-....
BER     .......... .........C .T...AG... .....G.... .C........ C.AC.A.... ....C-C...
HOL     .......... .........C .T..AAA..A .......... .C.......C C.A.C..... G.T.T-....
MAS     .......... ........AT .T.A.AA..A .......... .C.......A C.AT.T-A.. T...T-....
MEL     .C........ ........AT .T.A..G... .......... .C......T. C.G.AA.... .A..T-....
MUG     .C........ .........T .T.A.AG... .......... .C......TC C.A.CA.A.. GA..T-....
EL      ..T....... .......T.C .T..AAG... ....C..... .C.......G C.A.-.TC.. C....-....
ATH     .C........ .........C .T.A.AG... .....G.... .C.......C C.A.-..C.. GT..T-....
STR     .C........ .........C .T.A.AG... .....G.... .C.......C C.A.-..C.. GT..T-....
GAM     .-..-..... .----...AT .C.AAAG.A- .......... .C......TC C.TTA.TT.. GA..C-....
LEP     .......... ........AA .T..A.G... .......... .C........ T.A..A-G.A ....T-....
MOR     .......... .........CT .T..AAG... .....G.... .C.......C C.ACC..... G...C-....
DAC     .......... .........T .T...AG... ....C..... .C.......G C.T.GT...A GCG.GC....
MLI     .......... .......T.T .T..AAA... ....C..... .C......TC C.GCC..... GA..TT....
BOT     .......... .......T.A .T....G... .......... .C......TA C.ACGT..GA ..T...T...

                500         510         520         530         540         550         560
                 .           .           .           .           .           .           .

SYN     GGAAG----- GGACGCTGAA AA?CA--TCC --CC-CGAAG GCGGATTTAG CAGTAAGTCA GGAA-TAGAG
HYG     .A...A.... A..TA-.... ..GA-....T ..T....... .A........ ......C.GG ...G......
LAM     .A..AG.... ..T-.T.... ..CAC..A.. .....TA... .A........ .......AGG AA...C....
POL     .A.C.A.... T.T-A..... .TAT-..A.A ......A... .A........ ........A. AA.......
PERC    .A.T-A.... T.G-A..... .TCGC..C.A ..TT.TA... .A........ ........A. AA.-.C....
APH     TA.T.G.... TA.-AT.... .TA--...TA A....T.... .A........ ........AG AA...C....
PLL     .A.TTG.... TA.-TT.... ..AA-...TA .....T.... .A........ ........AG ..........
MER     .A.T.G.... CAG-C..... ..C.-..CTG .....T.... .T........ .......GGG ..........
PEX     ACGGATGG.. T..AA-.... .CAA-....A .......... .A........ ........AG AA.G.C....
OPS     .A..CAAG.. T..---.... .TAACAC.TA A.--.-.... .A........ A.......A. .TT-.C....
SB      .A.T.TAAAC AT.-..... .CG--...AT AA-..T.... .A........ -........GG AA.......A
ZEU     .A.T.GT... .TG--T.... .CA.C..CA. ..-..T.... .A........ ........GG TA........
ZNP     .A.TAGT... .TG---.... .CA--..CA. .A...T.... .A........ ........GG AA........
BER     .A.T.TATTA .T.--..... .CA--...A. AA-..T.... .A........ ........GG AA........
HOL     .A.TAA.... TACA-..... .CG.-..GTA ..TT.T.... .A.......A T.......AG AA........
MAS     .A.T.A.... TA.A-T.... .CA--...T. A.T..T.... .A........ ........CAG AA........
MEL     ...TTA.... T.TAA-.... ..C--..A.A ..TTAT.... .A........ T......CA. AA........
MUG     .A.T.A.... T.CA-..... .TAA-..G.A TATT.T.... .A........ ......A.G. AA.G.C....
EL      .A.C.A.... CA.AA-.... .TGT-...TG ..T..TA... .A........ A.......A. AA........
ATH     .A..AA.... T.CAA-.... .----..G.G ..TTA-.... .A........ T......CA. .A........
STR     .A..AA.... T.CAA-.... ..AA-..G.A ..TTA-.... .A........ .......AAG AA....C....
GAM     .A.TTG.... T.CTA-.... .TA--..A.A ..-.AT.... .T...-.... .......AA. AAG..---.-
LEP     .A.T.A.... TTGA-..... .C---..GT. TTT....... .A........ .......CAG .A........
MOR     .A.T.G.... CACA-T.... .TGT-..GTG TAT..T.... .A........ T......CAG A.........
DAC     CCG..CC... ATTAA..... ..TGTT..GG TA--.-..TT AA........ .......AG. .AG..?????
MLI     .A.T...... AT.TAT.... .TA--...AT GC.T.-.... .A........ T......AG. AA........
BOT     ...TA..... TCT..T.... .CATG..AGA TT--.-.... .A........ T.......GG AA...C....
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Fig. 2. *Continued.*

```
                570         580         590         600         610         620         630]
                .           .           .           .           .           .           .]
SYN     CGTCTGACTG AAATTTATCT GGTAAAGCGA ATGATTAGAG GTCTTGGGGC CGAAACGATC TCAACCTATT
HYG     ..C.CC.G.. .......... .......... .......... .......... .......... ..........
LAM     T..T.CC... ..G....... .......... .......... ..G....... .......... ..........
POL     ...T.T.... .......... .......... ....C..... ...A...... .......... ..........
PERC    T..T.T.... .......... .......... .......... ...A...... .......... ..........
APH     TT.TCC.... .......-.. .......... .......... ...A...... .......... ..........
PLL     T.A.CTG... .......... .......... ....C..... .C........ .......... ..........
MER     T.C.CCC... .......... .......... ....C..... .C........ .......... ..........
PEX     T..TCT.... .......... .......... ....C..... .C........ .......... ..........
OPS     TAA.CC.... .......... .......... ....C..... .C........ .......... ..........
SB      A...CC.... .......... .......... .......... .......... .......... ..........
ZEU     T...CC.... .......... .......... ....C..... .C........ .......... ..........
ZNP     .A..CC.... .......... .......... ....C..... .C........ .......... ..........
BER     ...TCC.... .......... .......... .......... .......... .......... ..........
HOL     T...CT.... .......... .......... .......... .C........ .......... ..........
MAS     ...TCTG... .......... .......... .......... .C........ .......... ..........
MEL     T..T.TG... .......... .......... .......... .......... .......... ..........
MUG     ...T.C.T.. .......... .......... .......... .C........ .......... ..........
EL      T..T.T.... .......... .......... .......... .......... .......... ..........
ATH     .....TG... .......... .......... .....G.... .......... .......... ..........
STR     T..TCT.A.. .......... .......... .......... .......... .......... ..........
GAM     -..TCCG... .......... .......... .......... .......... .......... ..........
LEP     T..TCTG... .......... .......... .......... .......... .......... ..........
MOR     T...CTG... ..C....... .......... .......... .......... .......... ..........
DAC     ?????????? ???....... .......... .......... .......... .......... ..........
MLI     A.CT..T... .......... .......... .......... .......... .......... ..........
BOT     T..TCCG... .......... .......... .......... .......... .......... ..........

                640         650         660         670         680         690         700
                .           .           .           .           .           .           .
SYN     CTCAAACTTT AAATGGGTAA GAAGCCCGGC TCGCTGGCTT GGAGCCG-GG CGTGGAATGC GAG-CGCCCA
HYG     .......... .......... ..G....... ....C.A..C .......... .......... ..........
LAM     .......... .......... ........A. .......... .......... .......... ..........
POL     .......... .......... .......... .......... .......... .......... ...C......
PERC    .......... .......... ..G....... .......... .......... ..C....... ...C......
APH     .......... .......... ..G....... .......... .......... ..C....... ...C......
PLL     .......... .......... ..G....T.. .......... .....A.... .......... ...T......
MER     .......... .......... ..G....T.. .......... .....A.... .......... ...T......
PEX     .......... .......... ...A...?.. .......... .......... .......... ...C....T.
OPS     .......... .......... .......... .......... .......... .......... ...C....T.
SB      .......... .......... .......... C......... ..G.....T. .......... ...C....T.
ZEU     .......... .......... .......T.. .......... .....A.... .......... ...A......
ZNP     .......... .......... .......T.. .......... .....A.... .......... ...A......
BER     .......... .......... .......... .......... .......... .......... ...C....T.
HOL     .......... .......... .......... .......... .......... .......... ...C....T.
MAS     .......... .......... .......... .......... .......... .......... ...C....T.
MEL     .......... .......... .......... .......... .......... .A.......T ...C....T.
MUG     .......... .......... .......... .......... .......... .......... ...C....T.
EL      .......... .......... .......... .......... .......... .A........ ...C......
ATH     .......... .......... .......... .......... .......T.. .A.......T ...C......
STR     .......... .......... .......... .......... .......... .......... ...C....T.
GAM     .......... .......... .......... .......... .......... .......... ...CT.....
LEP     .......... .......... .......... .......... .......... .......... ...C....T.
MOR     .......... .......... .......... .......... .......... .......... ...C....T.
DAC     .......... .......... .......... .......... .......... .......... ...C....-.
MLI     .......... .......... .......... .......... .......... .......... ...C....T.
BOT     .......... .......... .......... .......... .......... .......... ...C....T.
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Fig. 2. *Continued.*

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                 710        720        730        740        750        760        770
                  .          .          .          .          .          .          .

SYN      GTGGGCCACT TTTGGTAAGC AGAACTGGCG CTGCGGGATG AACCGAACGC CGGGTTAAGG CGCCCGATGC
HYG      .......... .......... .......... .......... .......... .......... ..........
LAM      .......... .......... .......... .......... .......... .......... ..........
POL      .......... .......... .......... .......... .......... .......... ..........
PERC     .......... .......... .......... .......... .......A.. .......... ..........
APH      .......... .......... .......... .......... .......A.. .......... ..........
PLL      .......... .......... .......... .......... .......... .......... ..........
MER      .......... .......... .......... .......... .......... .......... ..........
PEX      .......... .......... .......... .......... .......... .......... ..........
OPS      .......... .......... .......... .......... .......... .......... ..........
SB       .......... .......... .......... .......... .......... .......... ..........
ZEU      .......... .......... .......... .......... .......... .......... ..........
ZNP      .......... .......... .......... .......... .......... .......... ..........
BER      .......... .......... .......... .......... .......... .......... ..........
HOL      .......... .......... .......... .......... .......... .......... ..........
MAS      .......... .......... .......... .......... .......... .......... ..........
MEL      .......... .......... .......... .......... .......... .......... ..........
MUG      .......... .......... .......... .......... .......... .......... ..........
EL       .......... .......... .......... .......... .......... .......... ..........
ATH      .......... .......... .......... .......... .......... .......... ..........
STR      .......... .......... .......... .......... .......... .......... ..........
GAM      .......... .......... .......... .......... .......... .......... ..........
LEP      .......... .......... .......... .......... .......... .......... ..........
MOR      .......... .......... .......... .......... .......... .......... ..........
DAC      .......... .......... .......... .......... .......... .......... ..........
MLI      .......... .......... .......... .......... .......... .......... ..........
BOT      .......... .......... .......... .......... .......... .......... ..........


                 780        790        800        810        820        830        840
                  .          .          .          .          .          .          .

SYN      CGACGCTCAT CAGACCCCAG AAAAGGTGTT GGTTGATATA GA?AGCAGGA CGGTGGCCAT GTGGCGCTGG
HYG      .......... .........C .......... .......... ..C....... .......... ..........
LAM      .......... .......... .......... .......... ..C....... .......... ..........
POL      .......... .....A.... .......... .......... ..?....... .......... ..........
PERC     .......... .......... .......... .......... ..C....... .......... ....?.....
APH      .......... .......... .......... .......... .????????? ?????????? ?.........
PLL      .......... .......... .......... .......... ..C....... .......... ..........
MER      .......... .......... .......... .......... ..C....... .......... ..........
PEX      .......... .......... .......... ...C...... ..C....... .......... ..........
OPS      .......... .......... .......... ...C...... ..C....... .......... ..........
SB       .......... .......... .......... ...C...... ..C....... .......... ..........
ZEU      .......... .....A.... .......... .......... ..C....... .......... ..........
ZNP      .......... .....A.... .......... .......... ..C....... .......... ..........
BER      .......... .......... .......... ...C...... ..C....... .......... ..........
HOL      .......... .......... .......... ...C...... ..C......? ........?. ..........
MAS      .......... .......... .......... ...C...... ..C....... .......... ..........
MEL      .......... .......... .......... .......... ..T....... .......... ..........
MUG      .......... .......... .......... .......... ..C....... .......... ..........
EL       .......... .......... .......... .......... ..C......? .......... ..........
ATH      ..........G......... .......... .......... ..?....... .......... ..........
STR      .......... .......... .......... .......... ..T....... .......... ..........
GAM      .......... .......... .......... .......... ..A....... .......... ..........
LEP      .......... .......... .......... ...C...... ..C....... .......... ..........
MOR      .......... .......... .......... ...C...... .????????? ?????????? ?.........
DAC      .......... .......... .......... ...C...... ..C....... .......... ..........
MLI      .......... .......... .......... ...C...... ..C....... .......... ..........
BOT      .......... .......... .......... ...C...... ..C....... .......... ..........
```

Fig. 2. *Continued.*

```
                 850         860         870         880         890         900         910
                  .           .           .           .           .           .           .

SYN      AGCGTCGGGC CCATACCCGG CCGTCGCCGG CAGCGG-GA- GCC-TCGAGG GCTAGGCCGC GACGAGTAGG
HYG      .......... .......... ....A.TT.. .CA....A.T ....G..... ....C..... .........A
LAM      .......... .......... .......... ....AC.... ....A..... .......... ..........
POL      .......... .......... .......T.. ..A.A..... .......G.. ....T..... ..T.......
PERC     .......... .......... .......GC. .-A..A.... .......G.. ....C..... ..........
APH      .......... .......... .......GC. ..A..A.... .......G.. ....C..... ..T.......
PLL      G......... .......... .......T.. .GATC..... ....A..T.. ....C..... ..T.......
MER      .......... .......... .......T.. .GATC..... ....A..T.. ....C..... ..T.......
PEX      .......... .......... .......... ..A.A..... .......... .......... ..........
OPS      .......... .......... .......... ..A.A...G. ....G..... ....C..... ..........
SB       .......... .......... .......... ..CTA..... ....G..... ....C..... ..........
ZEU      .......... .......... .......... .GAG.A.C.. ....A..G.. ....C..... ..........
ZNP      .......... .......... .......... .GAG.A.C.. ....A..G.. ....C..... ..........
BER      .......... .......... .........? ..A.A..... ....G..... ....C..... ..........
HOL      .......... .......... .......... ..A.A..... ....G..... .......... ..........
MAS      .......... .......... .......T.. ..A.A..... .......... ....C..... ..........
MEL      .......... .......... .......... ..A..... ....G..... .......... ..........
MUG      .......... .......... .......... ..A..... ....G..... ....T..... ..........
EL       .......... .......... .......T.. ..A.AA.... ....G..... ....C..... ..T.......
ATH      .......... .......... .......T.. ...T..A... ...C.G...A ....T..... ..........
STR      .......... .......... .......... ....A..... ....G..... .......... ..........
GAM      .......... .......... ...C...... ..A.CA.... ....G..... .......... .GT.......
LEP      .......... .......... .......T.. ..A.A..... ....G..... ....C..... ..........
MOR      .......... .......... .......... ..A.A..... ....G..... ....T..... ..........
DAC      .......... .......... .......... .GA.A...G. ....G..... ....C..... ..........
MLI      .......... .......... .......... ..A.A...G. ....G..... .......... ..........
BOT      .......... .......... .......... ..A..... ....G..... .......... ..........


                 920         930         940         950         960         970         980
                  .           .           .           .           .           .           .

SYN      AGGGCCGCCG CGGTGCGCAC GGAAGCCCAG GGCGCGGGCC CG?GTGGAGC CGCCGCGGGT GCAGATCTTG
HYG      .......... .....-..G. .......T.. .......... ..G....... .......... ..........
LAM      .......... .......... .......T.. .......... ..G....... .......... ..........
POL      .......... .....A.... .......T.. ....T..... ..G....... .......... ..........
PERC     .......... .....A.... .......T.. .......... ..G....... .......... ..........
APH      .......... .......... .......T.. .......... ..G....... .......... ..........
PLL      .......... .....A.... .......T.. ....T..... ..G....... .......... ..........
MER      .......... .....A.... .......T.. .......... ..G....... .......... ..........
PEX      .......... .......... .......T.. .......... ..G....... .......... ..........
OPS      ....T..... .......... .......... .......... ..G....... .......... ..........
SB       .......... .....A.... .......T.. ....T..... ..G....... .......... ..........
ZEU      .......... .....A.... .......T.. .......... ..G....... .......... ..........
ZNP      .......... .....A.... .A.....T.. .......... ..G....... .......... ..........
BER      .......... .....A.... .......T.. ....T..... ..?....... .......... ..........
HOL      .......... .....A.... .......T.. ....T..... ..G....... .......... ..........
MAS      .......... .....A.... .......T.. .......... ..G....... .......... ..........
MEL      .......... .....A.... .......T.C .AG...-A.T ..G....... .......... ..........
MUG      .......... .....A.... .......T.. ......A... ..G....... .......... ..........
EL       .......... .....A.... .......T.. .......... ..G....... .......... ..........
ATH      C..A...T.. .......... T......T.. .......... ..G....... .......A.. ..........
STR      .......... .....A.... .......T.. ......A... ..G....... .......... ..........
GAM      .......... .....A.... .......T.. .......A.. ..G....... .......... ..........
LEP      .......... .....A.... .......T.. .......... ..G....... .......... ..........
MOR      .......... .....A.... .......T.. ....T..... ..G....... .......... ..........
DAC      .......... .....A.... .......T.. .......... ..G....... .......... ..........
MLI      .......... .....A.... .......T.. .......... ..G....... .......... ..........
BOT      .......... .......... .......... .......... ..G....... .......... ..........
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Fig. 2. *Continued.*

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                990        1000       1010       1020       1030       1040       1050
                 .          .          .          .          .          .          .

SYN     GTGGTAGTAG CAAATATTCA AACGAGAACT TTGAAGGCCG AAGTGGAGAA GGGTTCCATG TGAACAGCAG
HYG     .......... .......... .......... .......... .......... .......... ..........
LAM     ..A....... .......... .......... .......... .......... .......... ..........
POL     .......... .......... .......... .......... .......... .......... ..........
PERC    .......... .......... .......... .......... .......... .......... ..........
APH     .......... .......... .......... .......... .......... .......... ..........
PLL     .......... .......... .......... .......... .......... .......... ..........
MER     .......... .......... .......... .......... .......... .......... ..........
PEX     .A........ .......... .......... .......... .......... .......... ..........
OPS     .......... .......... .......... .......... .......... .......... ..........
SB      .......... .......... .......... .......... ....A..... .......... ..........
ZEU     .......... .......... .......... .......... ....T..... .......... .A........
ZNP     .......... .......... .......... .......... ....T..... .......... .A........
BER     .......... .......... .......... .......... .......... .......... ..........
HOL     .......... .......... .......... .......... .......AG. A.......... .A........
MAS     .......... .......... .......... .......... .......... .......... ..........
MEL     .......... .......... .......G.. .......... .......... .......... ..........
MUG     .......... .......... .......... .......... .......... .......... ..........
EL      .......... .......... .......... .......... .......... .......... ..........
ATH     .......... .......... .......G.. .......... .......... .......... ..........
STR     .......... .......... .......... .......... .......... .......... ..........
GAM     .......... .......... .......G.. .......... .......... .......... ..........
LEP     .......... .......... .......... .......... .......... .......... ..........
MOR     .......... .......... .......... .......... .......... .......... .A........
DAC     .......... .......... .......... .......... .......... .......... .T........
MLI     .......... .......... .......... .......... .......... .......... .A........
BOT     .......... .......... .......... .......... .......... .......... ..........


                1060       1070       1080       1090       1100       1110       1120
                 .          .          .          .          .          .          .

SYN     TTAGAGTTCT CTTTTCTTT- GTGAAGGGCA GGGCGCCCTG GAATGGGTTC GTCCCGAGAG AGGGGCCCGC
HYG     .......... .......... .......... .......... .......... .......... ..........
LAM     .......... .......... ..C....... .......... .......... .C........ ..........
POL     .......... .......... ..C....... .......... .......... .C........ ..........
PERC    .......... .......... ..C....... .......... .......... .C........ ..........
APH     .......... .......... .......... .......... .TT....... .C........ ........AA
PLL     .......... .......... .......... .......... .......... .C.......T .........T
MER     .......... .......... .......... .......... .......... .C.......T .........T
PEX     ........T. .......... .....T.... .......... .......... .C........ ..........
OPS     .......... .......... .....T.... .......... .......... .C........ ..........
SB      .......... .......... .......... .......... .......... .C........ .........T
ZEU     .......... .......... .......... .......... .......... .C.......T .........T
ZNP     .......... .......... .......... .......... .......... .C.......T .........T
BER     .......... .......... .......... .......... .......... .C........ ..........
HOL     .......... .......... .......... .......... .......... .C........ ..........
MAS     .......... .......... .......... .......... .......... .C........ .........T
MEL     .......... .......... .......... .......... .......... .C.......T .........T
MUG     .......... .......... .......... .......... .......... .C........ ..........
EL      .......... .......... .......... ....T..... .......... .C...T...T .........T
ATH     .......... .......... .......... .......... .......... .C.......T ..........
STR     .......... .......... .......... .......... .......... .C........ .........T
GAM     .......... .......... .......... .......... .......... .C........ ..........
LEP     .......... .........T .......... .......... .......... .C........ .........T
MOR     .......... .......... .......... .......... .......... .C........ .........T
DAC     .......... .....TC... .......... .......... .......... .C........ .........T
MLI     .......... .....TC... .......... .......... .......... .C........ .........T
BOT     .......... .....TC... .......... .......... .......... .C........ ..........
```

Fig. 2. *Continued.*

```
                1130        1140        1150        1160        1170        1180        1190
                  .           .           .           .           .           .           .

SYN     GCCCTGGAAA GCGTCGCGGT TCCGGCGGCG TCAGGTGAGC CTTCGCCGGC CCTTGAAAAT CCGGGGGAGA
HYG     .......... .......... .......A.. ..C..... TC..... .......... .....CC...
LAM     .......... .......... .......... ..C..... TC....T... .......... ..........
POL     .......... .......... .......... ..C..... TC....T... .......... ..........
PERC    .......... .......... ....C..T.. ..C..... TC....T... .......... ..........
APH     .......... .......... .......... ..C..... TC....T... .......... ...A......
PLL     .......... .......... .......... ..C..... T.....T... .......... .....T....
MER     .......... .......... .......... ..C..... TC....T... .......... .....T....
PEX     .......... .......... .......... ..C..... TC....T... .......... ..........
OPS     .......... .......... .......... ..C..... TC....T... .......... ..........
SB      .......... .......... .......... ..C..... TC....T... .......... ..........
ZEU     .......... .......... .......... ..C..... TC....T... .......... .....C....
ZNP     .......... .......... .......... ..C..... TC....T... .......... .....C....
BER     .......... .......... .......... ..C..... TC....T... .......... ..........
HOL     .......... .......... .......... ..C..... TC...T.... .......... ..........
MAS     .......... .......... .T........ ..C..... TC....T... .......... ..........
MEL     .......... .......... .......... ..C..... TC....T... .......... ..........
MUG     .......... .......... .......... ..C..... TC....T... .......... ..........
EL      ..T....... ...C.....C ..T....... ..C..... TC...T...T .......... ..........
ATH     .......... .......... ..T....... ..C.....A. TC....T... .......... ..........
STR     .......... .......... .......... ..C..... TC....T... .......... ..........
GAM     .......... .......... .......... ..C..... TC....T... .......... ..........
LEP     .......... .......... .......... ..C..... TC....T... .......... ..........
MOR     .......... .......... .......... ..C..... TC....T... .......... ..........
DAC     .......... .......... .......... ..C..... TC....T..T .......... ..........
MLI     .......... .......... .......... ..C..... TC....T... .......... ..........
BOT     .......... .......... .......... ..C..... TC....T... .......... ..........
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```
                1200        1210        1220        1230        1240        1250        1260
                  .           .           .           .           .           .           .

SYN     GGGTGTAAGT CTCGCGCCAG GCCGTACCCA TATCCGCAGC AGGTCTCCAA GGTGGACAGC CTCTGGCATG
HYG     A.......A. .......... .......... .......... .......... ....A..... ..........
LAM     A.......A. .......... A......... .......... .......... ....A..... ..........
POL     A.......A. .......... .......... .......... .......... ....A..... ..........
PERC    A.......A. .......... .......... .......... .......... ....A..... ..........
APH     T.......A. .......... .......... .......... .......... ....A..... ..........
PLL     A.......A. .......... .......... .......... .......... ....A..... ..........
MER     A.......A. .......... .......... .......... .......... ....A..... ..........
PEX     ........A. .......... .......... .......... .......... ....A..... ..........
OPS     ........A. .......... .......... .......... .......... ....A..... ..........
SB      A.......A. .......... .......... .......... .......... ....A..... ..........
ZEU     A.......A. .......... .......... .......... .......... ....A..... ..........
ZNP     A.......A. ........T. .......... .......... .......... ....A..... .......?..
BER     A.......A. .......... .......... .......... .......... ....A..... ..........
HOL     A.......A. .......... .......... .......... .......... ....A..... ..........
MAS     A.......A. .......... .......... .......... .......... ....A..... ..........
MEL     A.......A. .......... .......... .......... .......... ....A..... ..........
MUG     A.......A. .......... .......... .......... .......... ....A..... ......T...
EL      C.......A. .......... .......... .......... .......... ....A..... ..........
ATH     .......... ....TA.... .......... .......... .......... ....A..... .......G..
STR     A.......A. .......... .......... .......... .......... ....A..... .......G..
GAM     A.......A. .......... .......... .......... .......... ....A..... ..........
LEP     A.......A. .......... .......... .......... .......... ....A..... ..........
MOR     A.......A. .......... .......... .......... .......... ....A..... ..........
DAC     A.......A. .......... .......... .......... .......... ....A..... ..........
MLI     A.......A. .......... .......... .......... .......... ....A..... ..........
BOT     ........A. .......... .......... .......... .......... ....A..... .......G..
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Fig. 2. *Continued.*

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                1270        1280        1290        1300        1310        1320        1330
                 .           .           .           .           .           .           .

SYN     TTGGATCCAC GGTGAAATAC CACTACTCTT ATCGTTTTTT CACTTACCCG GTGAGGCGGG GAGGCGAGCC
HYG     ..A..A.A.. .......... .......... .........C .......... .......... ..........
LAM     ..A....A.. .......... .......... .......... .......... .......... ..........
POL     ..A...GA.. .......... .......... .......... .......... .......... ..........
PERC    ..A..CGA.. .......... .......... .......... .......... .......... ..........
APH     ..A....A.. .......... .......... .......... .......... .......... ..........
PLL     A....A.A.. .......... .......... .......... .......... .......... ..........
MER     A....A.A.. .......... .......... .......... .......... .......... ..........
PEX     ..A....A.. .......... .......... .......... .......... .......... ..........
OPS     .....A.A.. .......... .......... .......... .......... .......... ..........
SB      ..A..CAA.. .......... .......... .......... .......... .......... ..........
ZEU     .....A.A.. .......... .......... .......... .......... .......... ..........
ZNP     ....?????. .......... .......... .......... .......... .......... ..........
BER     ..A....A.. .......... .......... .......... .......... ...?...... ....?.....
HOL     ..A...AA.. .......... .......... .......... .......... .......... ..........
MAS     ..A...GA.. .......... .......... .......... .......... .......... ..........
MEL     .......A.. .......... .......... .......... .......... .......... ..........
MUG     ..A....A.. .......... .......... .......... .......... .......... .........T
EL      A.A...GA.. .......... .......... .......CC. .......T.. .......... ..........
ATH     .......A.. .T........ .......... ..A....... .......... .......... ..........
STR     .......A.. .......... .......... .......... .......... .......... ..........
GAM     ......GA.. .......... .......... .......... .......... .......... A.........
LEP     ..A....A.. .......... .......... .......... .......... .......... ..........
MOR     ..A....A.. .......... .......... .......... .......... .......... ..........
DAC     ..A..A.A.. .......... .......... .......... .......... .......... ..........
MLI     ..A....A.. .......... .......... .......... .......... .......... ..........
BOT     ..A..A.A.. .......... .......... .......CC. .......... .......... ..........

                1340        1350        1360        1370        1380        1390        1400
                 .           .           .           .           .           .           .

SYN     CCGAGCGGGC TCTCGCTTCT GGC-GTCCAA GCGCCCGGCC TCCGC--GCC GGGCGCG?CC CGCTCCGGGG
HYG     ..T....... .......... ...G..--.. ...G..?... C.?.T..... ..C....A.. ..........
LAM     .......... .....T.... ..T...-... A..G.....T CGA.G..... ..C..T.A.. ..........
POL     .......... .....T.... ..T...-... .......... .GG....... .......G.. ..........
PERC    ...C...... .....T.... ..A...-... .........? ??........ .......A.. ..........
APH     ...C...... .....T.... ..T...-... ...T.....G .......... ..A....A.. ..........
PLL     .......... .......... A.T...-... ..C......T .----..... ..C...AA.. ..........
MER     .......... .....T.... ..T...-... .TC.....T CT???..... ..C....A.. ..........
PEX     .......... .......... A.....-... .........? ?????..... .......A.. ..........
OPS     .......... .......... ......-... .......... C...A..... ?......A.. ..........
SB      .......... .......... ......-... .........T CT???..... .....T.A.. ..........
ZEU     .........T .....T.... ......-... .......... .GGC..... .......A.. ..TC......
ZNP     .........T .....T.... ......-... ...T...... .GGC..... .......A.. ..TC......
BER     .........? .......... ..T...-... .........T CTG?T..... .....T.A.. ..........
HOL     .......... .......... A.T...-... A..T..... C.G??..... .....T.A.. ..........
MAS     .......... .......... ..T...-... .......... CAG??..... .....T.A.. ..........
MEL     .......... .......... ..T...-... .........G .......... .....T.A.. ..........
MUG     .......... .....T.... A.....-... ...A...... C.GC?..... ..T..T.A.. ........??
EL      .......... .....T.... A.T...-... ...A.....A C.GC..... ..T..T.A.. ......C...
ATH     .AT..-.... .......... ..T...-... .........T CT.CAAG... .....T.A.. ..........
STR     ..C....... .......... C.....-... .........A C.TAG..... .....T.A.. ..........
GAM     TGT..T.... .....G.... ......-... .........? ...?..... .....T.A.. ..........
LEP     .........? .......... ..T...-... .......... C.G....... .......A.. ..........
MOR     .......... .......... ..T...-... .......... C.G??..... .....T.A.. ..........
DAC     .......... .......... ..T...-... .........T C.G??..... ...G.T.A.. ..........
MLI     .......... .....T.... ......-... ...G.....A C.......... ..C..T.A.. ..........
BOT     .......... .....T.... ......-... .......... .GG??..... .......A.. ........A.
```

Fig. 2. *Continued.*

```
                1410        1420        1430        1440        1450        1460        1470
                   .           .           .           .           .           .           .

SYN     ACAGTGGCAG GTGGGGAGTT TGACTGGGGC GGTACACCTG TCAAACGGTA ACGCAGGTGT CCTAAGGCGA
HYG     ......A... .......... .......... .......... .......... .......... T.........
LAM     .......... .......... .......... .......... .......... .......... ..........
POL     .......... .......... .......... .......... .......... .......... ..........
PERC    .......... .......... .......... .......... ......T... .......... ..........
APH     .......... .......... .......... .......... ......T... .......... ..........
PLL     ......A... .......... .......... .......... .......... .......... ..........
MER     .......... .......... .......... .......... .......... .......... ..........
PEX     .......... .......... .......... .......... .......... .......... ..........
OPS     .......... .......... .......... .......T.. .......... .......... ..........
SB      .......... .......... .......... .......... .......... .......... ..........
ZEU     ......A... .......... .......... .......... .......... .......... ..........
ZNP     ......A... .......... .......... .......... .......... .......... ..........
BER     .......... .......... .......... .......... .......... .......... ..........
HOL     .......... .......... .......... .......... .......... .......... ..........
MAS     .......... .......... .......... .......... .......... .......... ..........
MEL     .......... .......... .......... .......... .......... .......... ..........
MUG     .......... .......... .......... .......... .......... .......... ..........
EL      .......... .......... .......... .......... .......... .......... ..........
ATH     .......... .......... .......... .......... .......... .......... ..........
STR     .......... .......... .......... .......... .......... .......... ..........
GAM     .......... .......... .......... .......... .......... .......... ..........
LEP     .......... .......... .......... .......... .......... .......... ..........
MOR     .......... .......... .......... .......... .......... .......... ..........
DAC     .......... .......... .......... .......... .......... .......... ..........
MLI     .......... .......... .......... .......... .......... .......... ..........
BOT     .......... .......... .......... .......... .......... .......... ..........

                1480        1490        1500        1510        1520        1530        1540
                   .           .           .           .           .           .           .

SYN     GCTCAGGGAG GACAGAAACC TCCCGTGGAG CAGAAGGGCA AAAGCTCGCT TGATCTTGAT TTTCAGTATG
HYG     .......... .......... .......... .......... .....C.... ......A..C ..........
LAM     ....G..... .......... .......... .......... .......... .......... ..........
POL     .......... .......... .......... .......... .......... .......... ..........
PERC    .......... .......... .....A.... .......... .......... .......... ..........
APH     .......... .......... .....A.... .....?.... .......... .......... ..........
PLL     .......... .......... .......... .......... .......... .......... ..........
MER     .......... .......... .......... .......... .......... .......... ..........
PEX     .......... .......... .......... .......... .......... .......... ..........
OPS     .......... .......... .......... .......... .......... .......... ..........
SB      .......... .......... .......... .......... .......... .......... ..........
ZEU     .......... .......... .......... .......... .......... .......... ..........
ZNP     .......... .......... .......... .......... .......... .......... ..........
BER     .......... .......... .......... .......... .......... .......... ..........
HOL     .......... .......... .......... .......... .......... .......... ..........
MAS     .......... .......... .......... .......... .......... .......... ..........
MEL     .......... .......... .......... .......... .......... .......... ..........
MUG     .......... .......... .......... .......... .......... .......... ..........
EL      .......... .......... .......... .......... .......... .......... ..........
ATH     .......... .......... .......... .......... .......... .......... ..........
STR     .......... .......... .......... .......... .......... .......... ..........
GAM     .......... .......... .......... .......... .......... .......... ..........
LEP     .......... .......... .......... .......... .......... .......... ..........
MOR     .......... .......... .......... .......... .......... .......... ..........
DAC     .......... .......... .......... .......... .......... .......... ..........
MLI     .......... .......... .......... .......... .......... .......... ..........
BOT     .......... .......... .......... .......... .......... .......... ..........
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Fig. 2. *Continued.*

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                1550        1560        1570        1580        1590        1600        1610
                  .           .           .           .           .           .           .

SYN     AATACAGACC GTGAAAGCGG GGCCTCACGA TCCTTCTGAC TTTTTGGGTT TTAAGCAGGA GGTGTCAGAA
HYG     .G........ .......... .......... ........G. .......... ......G... ..........
LAM     .......... .......... ......G... .........A C......... .......... ..........
POL     .......... .......... .......... .........A ....G..... .......... ..........
PERC    .......... .C........ .......... ........G. ......A... .......... ..........
APH     .......... .......... .......... ........G. .......... .......... ..........
PLL     .G........ .........C .......... .........T G......... .......... ..........
MER     .G........ .........C .......... .........T G......... .......... ..........
PEX     .......... .......... .......... .......... .......... .......... ..........
OPS     .......... .......... .......... .......... .......... .......... ..........
SB      .......... .......... .......... .......... .......... .......... ..........
ZEU     .G........ .......... .......... .........T A......... .......... ..........
ZNP     .G........ .......... .......... .........T .......... .......... ..........
BER     .......... .......... .......... .......... .......... .......... ..........
HOL     .......... .......... .......... .......... .......... .......... ..........
MAS     .......... .......... .......... .......... .......... .......... ..........
MEL     .......... .......... .......... .......... .......... .......... ..........
MUG     .......... .......... .......... .......... .......... .......... ..........
EL      .......... .......... .......... .......... .......... .......... ..........
ATH     .......... .......... .......... .......... C...G..... .......... ..........
STR     .......... .......... .......... .......... .......... .......... ..........
GAM     .......... .......... .......... .......... .......... .......... ..........
LEP     .......... .......... .......... .......... .......... .......... ..........
MOR     .......... .......... .......... .......... .......... .......... ..........
DAC     .......... .......... .......... .......... .......... .......... ..........
MLI     .......... .......... .......... .......... .......... .......... ..........
BOT     .......... .......... .......... ........G. .......... .C........ ..........
```

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                1620        1630        1640        1650        1660        1670        1680
                  .           .           .           .           .           .           .

SYN     AAGTTACCAC AGGGATAACT GGCTTGTGGC GGCCAAGCGT TCATAGCGAC GTCGCTTTTT GATCCTTCGA
HYG     .......... .......... .......... .......... .......... .......... ..........
LAM     .......... .......... .......... .......... .......... .......... ..........
POL     .......... .......... .......... .......... .......... .......... ..........
PERC    .......... .......... .......... .......... ......???? ?????????? ??????????
APH     .......... .......... .......... .........? ?????????? ?????????? ??????????
PLL     .......... .......... .......... .......... .......... .......... ..........
MER     .......... .......... .......... .......... .......... .......... ..........
PEX     .......... .......... .......... .......... .......... .......... ..........
OPS     .......... .......... .......... .......... .......... .......... ..........
SB      .......... .......... .......... .......... .......... .......... ..........
ZEU     .......... .......... .......... .......... .......... .......... ..........
ZNP     .......... .......... .......... .......... .......... .......... ..........
BER     .......... .......... .......... .......... .......... .......... ..........
HOL     .......... .......... .......... .......... .......... .......... ..........
MAS     .......... .......... .......... .......... .......... .......... ..........
MEL     .......... .......... .......... ......A... .......... .......... ..........
MUG     .......... .......... .......... .......... .......... .......... ..........
EL      .......... .......... .......... .......... .......... .......... ..........
ATH     .......... .......... .......... .......... .......... .......... ..........
STR     .......... .......... .......... .......... .......... .......... ..........
GAM     .......... .......... .....A.... .......... .......... .......... .........?
LEP     .......... .......... .......... .......... .......... .......... ..........
MOR     .......... .......... .......... .......... .......... .......... ..........
DAC     .......... .......... .......... .......... .......... .......... ..........
MLI     .......... .......... .......... .......... .......... .......... ..........
BOT     .......... .......... .......... .......... .......... .......... ..........
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Fig. 2. *Continued.*

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                1690        1700        1710        1720]
                  .           .           .           .

SYN      TGTC001000 0000000000 0000000000 0000000100 00
HYG      ....000000 0000000000 0000000001 0000000100 00
LAM      ....011111 1000110001 0011000000 1001000010 00
POL      ....111111 1111100000 0000000000 0000010000 00
PERC     ????111111 1111111100 0001010000 0000111100 00
APH      ????111111 1111111100 0001010000 0000111100 00
PLL      .???011110 1201111101 0031020020 1101121100 00
MER      ....011110 1211111101 0021020020 1001121100 00
PEX      ....011111 1111111111 0111000011 1101121100 00
OPS      ....111111 1111111121 0323220000 1101121100 00
SB       ....111111 1111111111 1000000001 1000100100 00
ZEU      ....111111 1111111111 0042020021 1000201100 01
ZNP      ....111111 1111111101 0241020021 1100101100 01
BER      ....110111 1111111121 1111111101 1000000000 10
HOL      ....111111 1111111121 1111111101 1000000020 10
MAS      ....11111? 11?11111?? ?321220?21 1?0?1221?1 00
MEL      ....111111 1111111121 1131220211 1101122111 00
MUG      ....111111 1111111121 1101210211 1111122121 00
EL       ....111111 1111111121 1131120221 1101122121 00
ATH      ....111111 1111111121 1131220211 1101122111 00
STR      ....011111 1111111101 0131020221 1101122111 00
GAM      ????011111 1111111101 0131020221 1101122111 00
LEP      ....111111 1111111121 1111110111 1111121120 00
MOR      ....111111 1111111121 1111111111 1111121120 00
DAC      ....111111 1211111121 1323220?01 1101121120 00
MLI      ....111111 1210111121 0133020021 1101121120 00
BOT      ....011111 1110111100 0140020321 1110121120 00
```

Fig. 2. Aligned DNA sequences and morphological data for 25 acanthomorph and two outgroup species. Taxon abbreviations are in Table 1.

3. Results

A total of 1722 transformation series (TS) for 25 acanthomorph and two outgroup taxa were obtained after alignment of the DNA sequences and integration of the morphological and molecular data (Fig. 2). There were a greater number of variable 12S rDNA sites (251 of 572 bp, 33% total) than 28S rDNA sites (178 of 1112 bp, 16% total).

Alignments of the 12S rDNA sequence are shown in Fig. 2, TS 1-572. Stem regions comprise the following transformation series: 1–4, 11–14, 18–20, 40–45, 52–56, 80–84, 100–101, 106–107, 109–114, 123–125, 132–135, 140–143, 145–146, 150–151, 155–158, 168–171, 175–178, 180–182, 194–197, 215–218, 220–223, 225–227, 235–239, 243–246, 250–253, 257–259, 262–274, 283–286, 289–298, 302–305, 314–317, 326–332, 346–362, 367–368, 373–375, 380–382, 395–396, 421–423, 425–427, 431–438, 443–450, 453–463, 469–472, 479–482, 501–503, 518–520, 536–540, 546–550, and 565–569. Inspection of loop regions lead us to discriminate between two classes of loops: (1) conserved loop regions and (2) non-conserved loop regions. Conserved loop regions are characterized by few gaps and relatively unambiguous alignments. These comprise TS 5–10, 15–17, 46–51, 57–79, 85–99, 102–105, 126–131, 136–139, 147–149, 152–154, 159–167, 172–174, 183–193, 219, 228–234, 240–242, 247–249, 254–256, 260–261, 275–282, 287–288, 299–301, 306–313, 318–325, 363–366, 369–372, 376–379, 388–394, 424, 428–430, 439–442, 451–452, 464–468, 489–494, 507–511, 527–535, 541–545, 551–564, and 570–573. Non-conserved loop regions are characterized by large gaps and

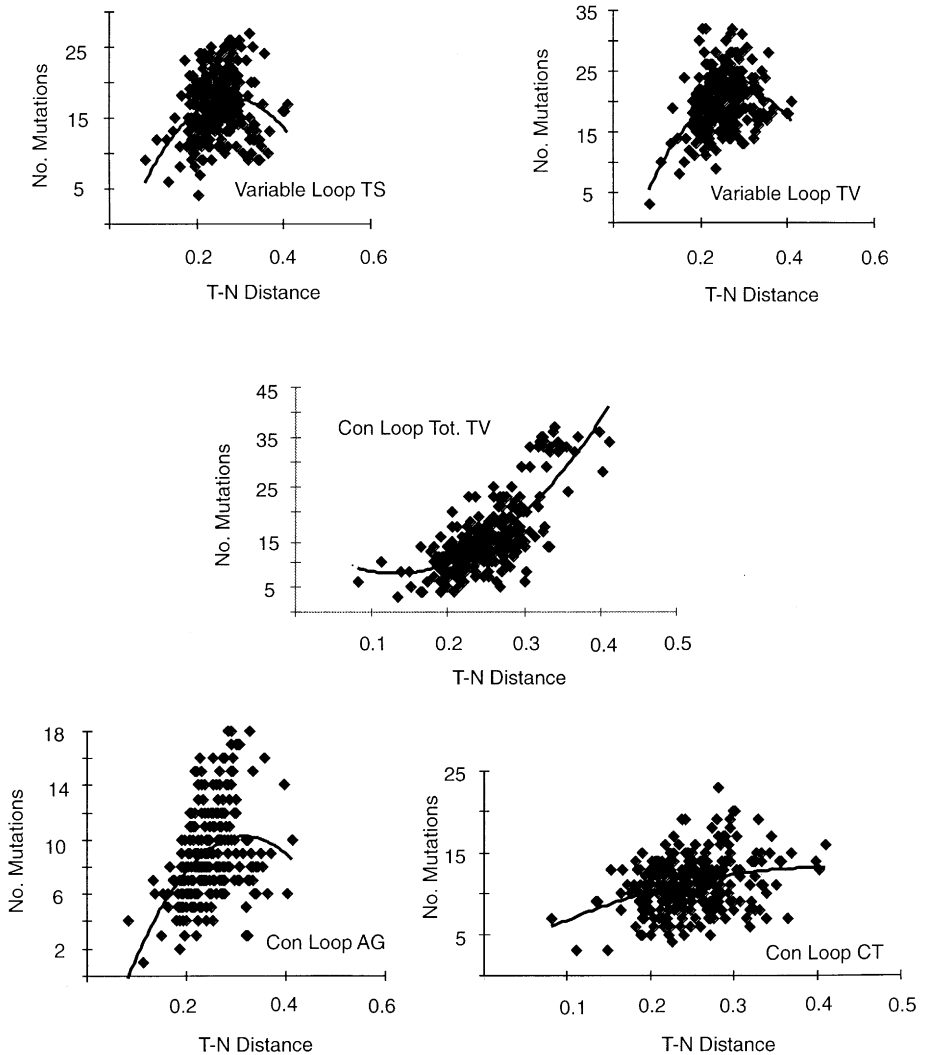

Fig. 3. 12S rDNA saturation study I. Pair-wise Tamura-Nei distances plotted against number of mutations for 25 species of acanthomorph fishes and two outgroups for loop regions. Above: Variable loop transistion (TS) and transversion (TV) plots. Middle: Conserved loop transversions. Bottom: Conserved loop transitions plots for arginine–guanine (AG) and cytosine–thymine (CT). A second-order polynominial trend line is fitted to the data in each plot.

ambiguous alignments. These comprised TS 21–39, 108, 115–122, 126–131, 144, 179, 198–214, 224, 333–345, 383–387, 397–421, 473–478, 483–488, 495–500, 512–517, and 521–526.

Plots of number of mutations versus Tamura-Nei Distance for the three classes of 12S rDNA data are shown in Figs. 3 and 4. We conclude that (1) both transitions and

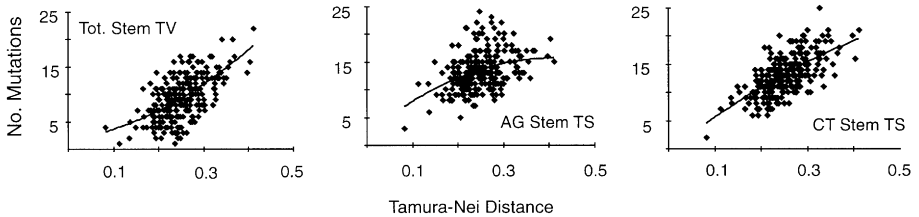

Fig. 4. 12S rDNA saturation study II. Pair-wise Tamura-Nei distances plotted against number of mutations for 25 species of acanthomorph fishes and two outgroups for stem regions. Left: Total transversions (TV). Middle: Arginine–guanine transitions (TS). Right: Cytosine–thymine transitions. A second-order polynominial trend line is fitted to the data in each plot.

transversions are saturated in the non-conserved loop regions, (2) both classes of transitions are saturated in the conserved loop regions, and (3) A–G transitions are saturated in the stems. Thus, nonconserved loops were eliminated from further analysis and step matrices were employed that screened classes of saturated mutations from further analysis in conserved loop and stem regions.

Data from four noncontiguous regions of the 28S rDNA gene were collected (Fig. 2). From 5′ to 3′ they were: 28ff (TS 573–831), 28ee (TS 832–1052), 28mm (TS 1053–1269), and 28wx (TS 1270–1684: see Hillis and Dixon, 1991). Alignment of the 28S rDNA was trivial. However, one region (TS 1371–1378) was largely unreadable and was eliminated from subsequent analyses. Stems comprised the following TS: 592–594, 597–601, 604–609, 611–612, 616–617, 619–627, 632–634, 655–662, 672–679, 682–691, 695–698, 705–708, 710–714, 720–724, 726–729, 734–736, 743–745, 749–754, 756–757, 759–761, 770–778, 794–796, 798–807, 815–819, 821–823, 827–828, 840–851, 854–861, 863–866, 868–871, 873–876, 892–903, 909–918, 920–925, 927–928, 935–936, 938–939, 942–943, 948–949, 951–952, 954–955, 959–969, 971–972, 997–1002, 1010–1015, 1017–1019, 1024–1041, 1053–1054, 1059–1063, 1065–1072, 1076–1079, 1081–1082, 1085–1089, 1098–1100, 1108–1110, 1112–1120, 1122–1123, 1134–1136, 1138–1139, 1142–1148, 1163–1171, 1174–1176, 1200–1205, 1207–1211, 1234–1243, 1249–1252, 1254–1257, 1260–1265, 1280–1284, 1286–1303, 1307–1311, 1315–1331, 1337–1349, 1361–1369, 1378–1386, 1390–1400, 1403–1420, 1423–1426, 1430–1441, 1453–1460, 1465–1481, 1489–1497, 1513–1521, 1524–1526, 1529–1532, 1540–1543, 1546–1553, 1557–1561, 1572–1582, 1593–1602, 1611–1615, 1619–1624, 1638–1643, 1661–1666, and 1680–1684. Loops comprised the remaining tranformation series. Three classes of mutations were investigated for saturation, AG and CT transitions and total transversions (Fig. 5). Based on plots of Tamura–Nei distances versus number of mutations, we conclude that 28S rDNA stems are saturated for A–G transitions while the loops are saturated for C–T transitions. These classes of mutations were screened from further analysis through the use of step matrices.

Variation among taxa for the 38 morphological transformation series is shown in Fig. 2. They comprise transformation series 1686–1722.

A series of parsimony analyses was performed, both on the total evidence matrix and partitioned subsets of the data. In each case, *Hygophum* was designated the operational sister group of Acanthomorpha and *Synodus* was designated the second

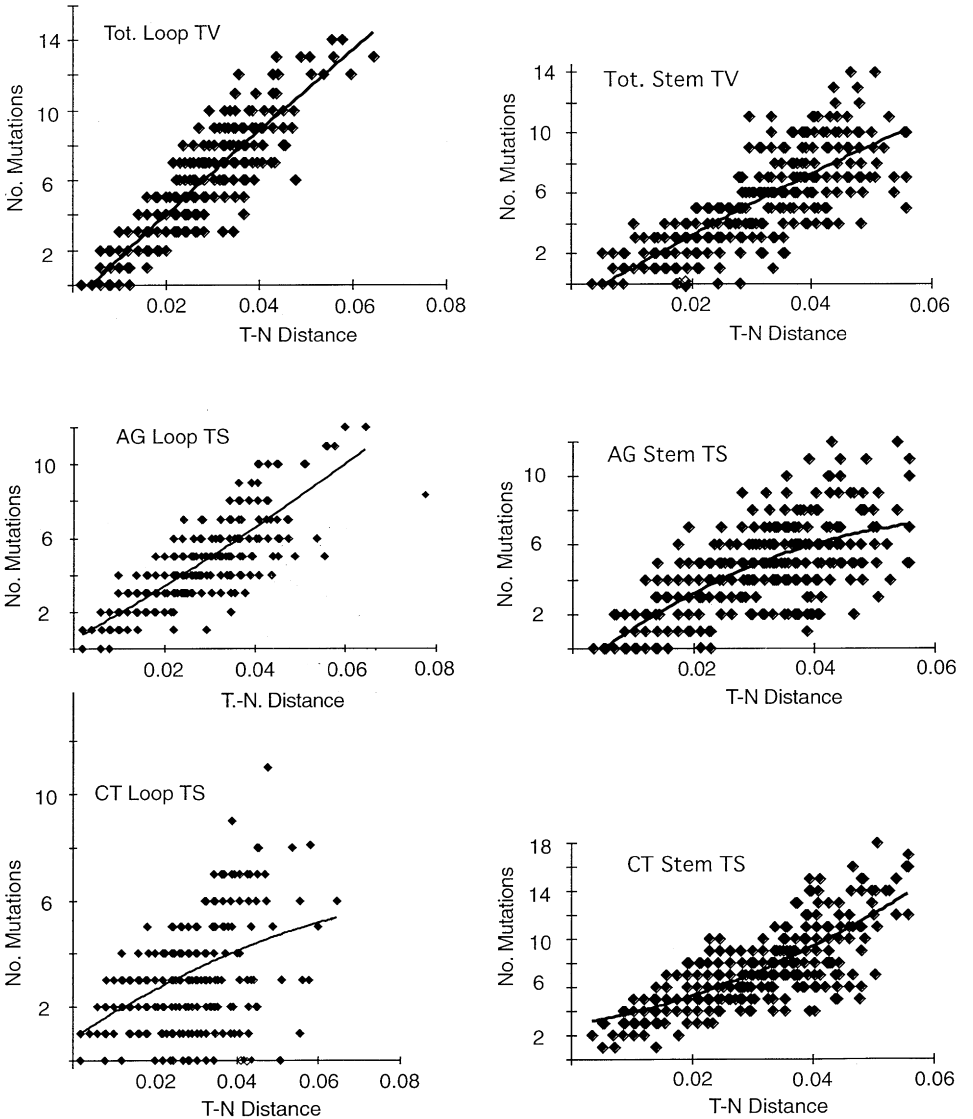

Fig. 5. 28S rDNA saturation study. Pair-wise Tamura-Nei distances and number of muitations for 25 species of acanthomorph fishes and two outgroups. Left side, top to bottom: Total loop transversions (TV), arginine–guanine (AG) loop transitions (TS), and cytocine–thymine (CT) loop transitions. Right side, top to bottom: Total stem transversions, AG stem transitions, and CT stem transitions. A second-order polynominial trend line is fitted to the data in each plot.

outgroup as per previous hypotheses of higher teleost relationships. Summary data for each analysis is shown in Table 3.

The total evidence analysis found four most parsimonious trees of 977 steps. A strict consensus tree was generated that reflects the 22 putative monophyletic groupings

Table 3
Summary of Tree "statistics" and characters for trees found in this study

	Analysis			
	Total evidence	12S rDNA	28S rDNA	Morphology
Parameter				
No. trees	4	6	23	137
Tree length	997 steps	580 steps	259 steps	116 steps
Ensemble CI	0.4724	0.4310	0.6371	0.4828
Ensemble HI	0.6422	0.5690	0.3629	0.5172
Ensemble RI	0.4605	0.6846	0.5251	0.7297
Ensemble RC	0.2176	0.3878	0.3572	0.3523
No. TS	1722	572	1112	38
TS excluded	136	124	12	0
TS informative	256	142	76	38
TS uninformative	213	109	104	0

Note: Excluded, informative, and uninformative refer to the number of characters in each class of data.

common to each of the most parsimonious trees (Fig. 6). A summary of branch lengths, number and quality of synapomorphies, Bremer support values and bootstrap values for each node appearing on the strict consensus tree is shown in Table 4. A summary of previously named groups that appear on the strict consensus tree is shown in Table 5. The four equally parsimonious trees differed primarly in their interpretations of the phylogenetic positions of *Elassoma* and *Mastacembelus*, as shown in the four subtrees in Fig. 7a–d.

Analysis of the 12S rDNA data alone resulted in six equally parsimonious trees whose strict consensus is shown in Fig. 8a. Analysis of the 28S rDNA data resulted in 23 equally parsimonious trees (consensus in Fig. 8b) while that of the morphological data resulted in 113 equally parsimonious trees (consensus in Fig. 8c).

4. Discussion

We expected that a combination of mitochondrial and nuclear ribosomal genes would provide a strong data base from which we could evaluate acanthomorph relationships. This expectation was only partly met. Saturation studies indicate that many of the regions of the 12S ribosomal gene useful in studies at lower taxonomic levels (Wiley et al., 1998; Tang et al., 1999) are saturated, especially in loop regions where only transversions could be used and then only for the "conserved loops." The 28S rDNA gene fragments were very conservative. Many of the few sites that do vary in the 28s rDNA regions we studied also show signs of transition saturation and those that do not are not of particular help in evaluating hypotheses unless used in a total evidence context. Given these observations, we might conclude that the DNA data

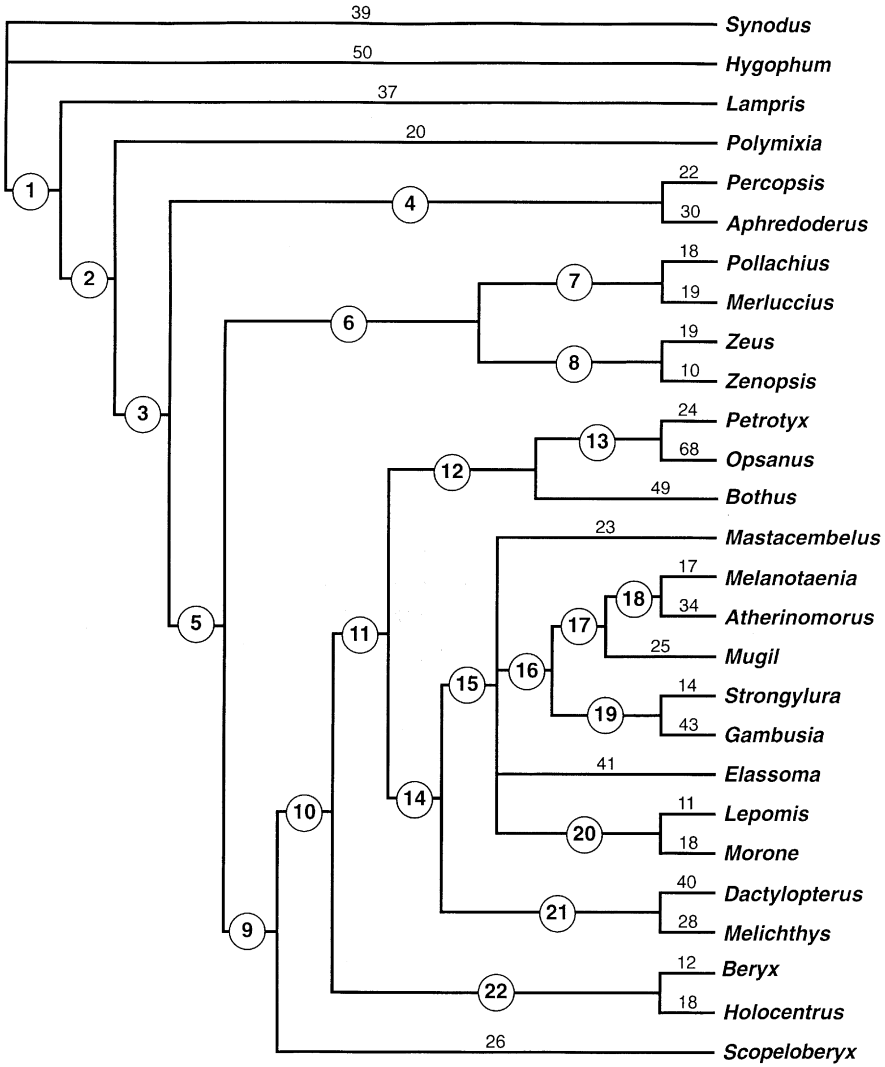

Fig. 6. A strict consensus tree of four equally parsimonious trees for 25 acanthomorphs under the constraint that *Synodus* and *Hygophum* are sequential outgroups. Numbers above terminal branches are branch lengths. Internode labels designate putative monophyletic groups. Tree summaries are shown in Tables 3 and 4.

played a relatively small role in the total evidence analysis. But, the morphological data, analyzed separately, did little better (Fig. 8c). Thus, we find it a remarkable consequence of character interactions within a total evidence analysis that we obtained any interpretable results at all, much less results that corroborate many of the conclusions of Johnson and Patterson (1993).

Table 4
Distribution of synapomorphies on strict consensus of four most parsimonious trees for acanthomorph fishes (Fig. 6)

Node	bl	ci = 1	ci > 0.49	ci < 0.5	Bremer	Bootstrap
1	13	6	1	6	8	100
2	15	1	3	11	6	84
3	7	2	2	3	1	61
4	17	5	4	8	9	92
5	4	0	1	3	1	51
6	15	2	4	9	7	94
7	27	3	10	14	19	100
8	21	7	2	12	12	100
9	14	0	2	12	5	85
10	5	0	1	4	1	< 50
11	6	0	2	4	1	< 50
12	5	0	0	5	1	< 50
13	13	1	3	9	5	61
14	7	0	0	7	1	< 50
15	2–6	0	1–3	1–4	1	< 50
16	6–8	0	1–2	5–6	3	58
17	5–6	0	0	5–6	2	< 50
18	8–9	1	1	6–7	3	76
19	11–12	0	1	10–11	5	86
20	9–11	1	1–2	7–9	4	65
21	11–13	1	6	4–6	2	< 50
22	11–12	1	3	7–8	4	58

Nodes with variable numbers reflect differences in support among the most-parsimonious trees for a particular internode. Abbreviations: bl, branch length; ci = 1, total unique and unreversed synapomorpies; ci > 0.49 and ci < 0.5, total synapomorphies with consistency indices greater or lesser than the value indicated; Bremer, the Bremer support value; Bootstrap, the bootstrap value.

Table 5
Previously recognized groups that appear on the strict consensus tree (Fig. 6)

Node	Clade	Previously recognized by
1	Acanthomorpha	Rosen (1973)
2	Euacanthomorpha	Johnson and Patterson (1993)
3	Holacanthopterygii	Johnson and Patterson (1993)
4	Percopsiformes	Berg (1947)
7	Gadiformes	Berg (1947)
8	Zeidae	Starks (1898)
14	Percomorpha	Johnson and Patterson (1993)
16	unnamed	Stiassney (1993)
18	Atherines	Dyer and Chernoff (1996)
19	Cyprinodontea	Dyer and Chernoff (1996)
20	Perciformes	Berg (1947)
22	Beryciformes	Johnson and Patterson (1993)

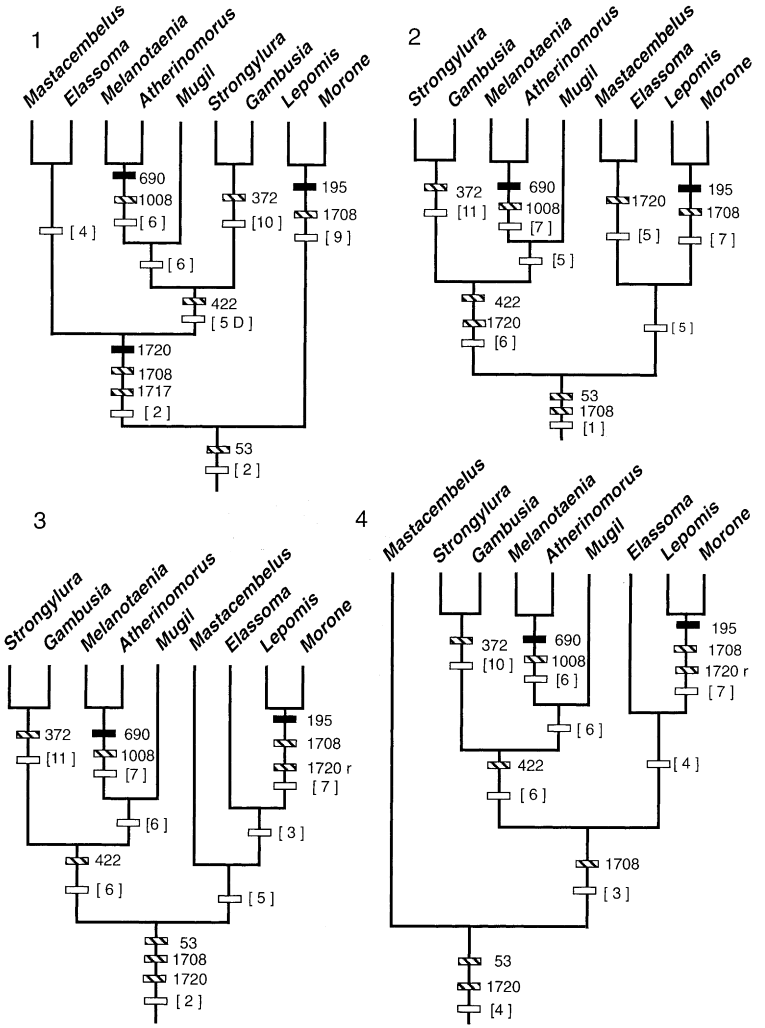

Fig. 7. Partial topologies of the four equally parsimonious trees found in this study. More basal topological relationships are identical although nodal support might vary. Black bars are unambiguous synapomorphies (ci = 1). Striped bars are synapomorphies with intermediate ci values (ci > 0.49). The total number of synapomorphies with low ci-values (ci < 0.5) is shown in brackets beside the white bars.

As noted, our selection of taxa differs substantially from that of Johnson and Patterson (1993), and these differences undoubtably account for some of the incongruence between their results and ours. We included several groups of Paracanthopterygii which Johnson and Patterson (1993) had represented only by the basal genus *Percopsis*, and, we included more nominal percomorphs in our formal analysis. Furthermore, Johnson and Patterson's (1993) discussion of morphological character variation is more extensive than ours and their taxon selection for the formal analysis

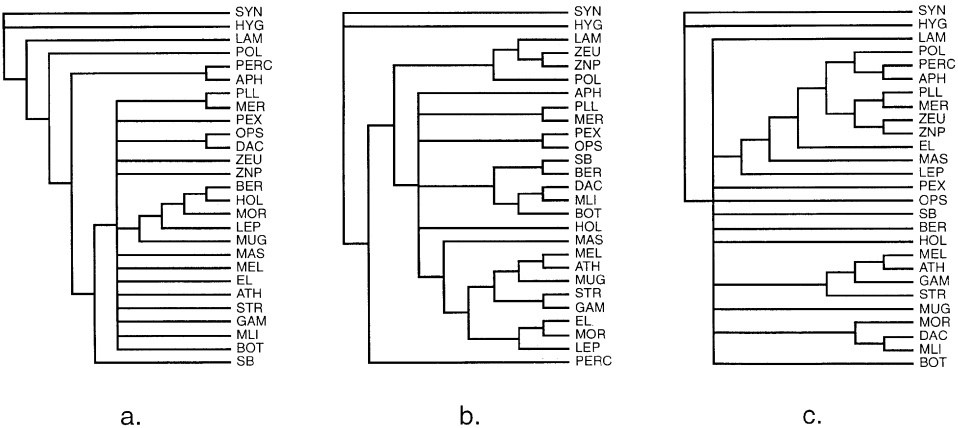

Fig. 8. Results from partitioned data sets. (a) The 12S rDNA data. A strict consensus tree of six equally parsimonious trees (tree length 580 steps, CI = 0.4310, HI = 0.5690, RI = 0.3878, RC = 0.1671). (b) The 28S rDNA data. A strict consensus tree of 23 equally parsimonious trees (tree length 259 steps, CI = 0.6371, HI = 0.3629, RI = 0.5607, RC = 0.3572). (c) Morphology data. Strict consensus of 137 equally parsimonious trees (tree length 116 steps, CI = 0.4828, HI = 0.5172, RI = 0.7297, RC = 0.3523).

was made from those taxa thought to be basal members of groups while our selection was made on the basis of available frozen material. Thus, our analysis is best viewed as an independent test of the morphological data ("nonoptimal" taxon selection), and an expansion of the parsimony analysis in terms of certain groups (paracanthopterygians, percomorphs) and characters (molecular data).

The overall topology of the strict consensus tree corroborates the basal position of Lampridiformes despite the fact that *Lampris* exhibits several characters that are interpreted as convergent similarities with higher acanthomorphs. These are TS 1696, character 1 (1696–1), 1700–1, 1704–1, 1711–1, 1714–1. In contrast, *Velifer* has the outgroup conditions (character "0" for each TS: Johnson and Patterson, 1993). Euacanthomorph monophyly is strongly corroborated (Bremer Support, $b = 6$), but *Polymixia* is only weakly corroborated as a basal euacanthopmorh ($b = 1$) because many of the potential synapomorphies of Euacanthomorpha are convergent in *Lampris*. Support would have been stronger if *Velifer* was used as a representative lampridiform fish. Strong to moderate corroboration for the monophyly of many long-recognized taxa was expected and found (Tables 4 and 5). These include Percopsiformes (*Percopsis* and *Aphredoderus*), Gadiformes (*Pollachius* and *Merluccius*), Zeidae (*Zeus* and *Zenopsis*), Beryciformes s.s. (*Holocentrus* and *Beryx*), Mugilomorpha + Atherinomorpha, and Perciformes (*Lepomis* and *Morone*).

Some general features of our topology are similar to the Johnson and Patterson (1993) hypothesis and different from those of previous authors, but these must be viewed with caution because low branch support values are associated with many nodes. Zeids (*Zeus* and *Zenopsis*) appear basally as hypothesized by Johnson and Patterson (1993), not near the apex as they would be expected to group given previous

hypotheses that they are related to beryciforms and percomorphs (Rosen, 1973, 1985). *Scopeloberyx* is basal to Beryciformes s.s. and these groups are basal to Percomorpha (Johnson and Patterson, 1993), contrary to most previous authors (see section Introduction). Smegmamorpha (Johnson and Patterson, 1993) is allied with "higher percomorphs" (i.e. perciforms, scorpaeniforms, tetraodontiformes, and pleuronectiforms) rather than being basal to a beryciform + percomorph clade (Rosen, 1973).

One major feature of our topology differs from that of Johnson and Patterson (1993). Zeids appear more basal than *Scopeloberyx*. This may be the result of not analyzing a stephanoberycid, since melamphaids such as *Scopeloberyx* share a number of derived characters with acanthopterygian fishes that are not shared by stepahnoberycids (see data matrix of Johnson and Patterson's (1993; p. 619)).

Morphological evidence for the monophyly of Paracanthopterygii (summarized by Patterson and Rosen, 1989) is tenuous at best (Gill, 1997). Paracanthopterygii appears polyphyletic on the strict consensus tree, with Percopsiformes and Gadiformes appearing more basally and the ophidiiform (*Petrotyx*) and batrachoidiform (*Opsanus*) grouping within Percomorpha. This result questions the monophyly of the group. It also questions the intrarelationships of its component members, since Patterson and Rosen (1989) hypothesized that gadiforms are closely related to batrachoidiforms, with ophidiiforms occupying a more basal position.

Finally, some of our results were unexpected. One of the more strongly corroborated groupings allies zeids with gadiforms, a hypothesis no one has proposed. A poorly corroborated node aligns *Petrotyx* and *Opsanus* with the pleuronectiform *Bothus*. This may be partly explained by our taxon selection because the most basal pleuronectiform, *Psetoddes*, has some of the synapomorphies of higher percomorphs that are lacking in *Bothus*. Other suspect and poorly supported nodes include the placement of *Mugil* within Atherinomorpha rather than as the sister group of a monophyletic Atherinomorpha, the grouping of *Dactylopterus* and *Melichthys*, and the basal position of this group relative to the smegmamorph and perciform fishes.

The newest and most controversial group of acanthomorphs, Smegmamorpha, does not appear as a monophyletic group in the strict consensus tree (Fig. 6). One of the most parsimonious trees does contain a monophyletic Smegmamorpha (Fig. 7a) and none of the alternative hypotheses (Fig. 7b–d) contain alternative hypotheses that are as strong in character support. However, we await a stronger test using more taxa and different genes to determine if independent molecular evidence can provide stronger corroboration or refutation for this clade. It is notewrothy that *Elassoma* did not group with its supposed centrarchid relative *Lepomis*. Although our analysis does not resolve the precise relationships of *Elassoma*, it suggests that *Elassoma* is not a centrarchid.

The results obtained in this study do not support several alternative hypotheses of relationships proposed by other authors. Holocentrids (*Holocentrus*) do not appear as the sister group of "higher percomorphs" (*Lepomis*, *Morone*, *Dactylopterus*, *Melichthys*, *Bothus* in our sample) as proposed by Stiassny and Moore (1992). No paracanthopterygian appears to be closely related to atherinomorphs (Parenti, 1993). Other

hypotheses not formally analyzed by Johnson and Patterson (1993) are corroborated. These include Stiassny's (1993) hypothesis that mullets are related to atherinomorphs and Dyer and Chernoff's (1996) hypothesis that rainbowfishes (*Melanotaenia*) and silversides (*Atherinomorus*) form a monophyletic group rather than being paraphyletic relative to other antherinomorphs (*Strongylura* and *Gambusia)*.

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References

Berg, L. 1947. Classification of Fishes Both Recent and Fossil. J. W. Edwards, Ann Arbor, Michigan, 517pp.

Bremer, K., 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42, 795–803.

Bremer, K., 1994. Branch support and tree stability. Cladistics 10, 295–304.

Clark, C.G., Tagve, B.W., Gerbi, S.A., 1984. *Xenopus laevis* 285 ribosomal RNA: a secondary structure model and its evolutionary and functional implications. Nucleic Acids Res 12 (15), 6197–6220.

Dyer, B.S., Chernoff, B., 1996. Phylogenetic relationships among atheriniform fishes (Teleostei: Atherinomorpha). Zool. J. Linnean Soc. London B 117, 1–69.

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

Fink, W.L., 1984. Basal euteleosts: Relationships. In: Moser, H.G. (Ed.), Ontogeny and Systematics of Fishes. American Society Ichthyologists and Herpetologists Spec. Publ. Allen Press, Lawrence, Kansas, pp. 202–206.

Fink, W.L., Weitzman, S.H., 1982. Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos*. Bull. Mus. Comp. Zool. 150, 31–93.

Gill, A.C., 1997. Comments on an intercalar path for the glossopharyngeal (Cranial IX) nerve as a synapomorphy of the Paracanthopterygii and on the phylogenetic position of the Gobiesocidae (Teleostei: Acanthomorpha). Copeia 1997 (4), 1022–1029.

Hillis, D.M., Dixon, M.T., 1991. Ribosomal DNA: molecular evolution and phylogenetic inference. Q. Rev. Biol. 66, 411–453.

Johnson, G.D., 1992. Monophyly of the euteleostean clades-Neoteleostei, Eurypterygii, and Ctenosquamata. Copeia (1) 1992, 8–25.

Johnson, G.D., Patterson, C., 1993. Percomorph phylogeny: a survey of acanthomorph characters and a new proposal. Bull. Mar. Sci. 52, 554–626.

Johnson, G.D., Patterson, C., 1996. Relationships of lower euteleostean fishes. In: Stiassny, M.L.J., Parenti, L.R., Johnson, G.D. (Eds.), The Interrelationships of Fishes. Academic Press, San Diego, California, pp. 251–331.

Kumar, S., Tamura, K., Nei, M., 1993. MEGA: Molecular Evolutionary Genetics Analysis (1.01). The Pennsylvania State University, University Park, PA.

Kocher, T.T., Meyer, A., Edwards, S., Paabo, S., Villablanca, F., Wilson, A., 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. Proc. Natl. Acad. Sci. USA 86, 6196–6200.

Lauder, G.V., Leim, K.F., 1983. The evolution and interrelationships of the actinopterygian fishes. Bull. Comp. Mus. Zool. 150, 95–197.

Leviton, A.E., Gibbs, R.H., Heal, E., Dawson, C.E., 1985. Standards in hertelology and Ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and Ichthyology. Copeia 1985, 802–832.

Maddison, D.R., 1991. The discovery and importance of multiple islands of most-parsimonious trees. Syst. Zool. 40, 315–328.

Maniatis, T., Fristch, E.F., Sambrook, J., 1982. Molecular Cloning. A Laboratory Manual. Cold Spring Harbor Laboratory, Cold Spring, NY.

Parenti, L.R., 1993. Relationships of atherinomorph fishes (Teleostei). Bull. Mar. Sci. 52, 170–196.

Patterson, C., Rosen, D.E., 1989. The Paracanthopterygii revisited: order and disorder. In: Cohen, D.M. (Ed.), Papers on the Systematics of Gadiform Fishes. Natural History Museum of Los Angeles County, Los Angeles, California, pp. 5–36.

Rosen, D.E., 1973. Interrelationships of higher euteleostean fishes. In: Greenwood, P.H., Miles, S., Patterson, C. (Eds.), Interrelationships of Fishes. J. Linn. Soc. (London) 53 Supplement 1. Academic Press, New York, pp. 397–513.

Rosen, D.E., 1985. An essay on euteleostean classification. Am. Mus. Novit. 2827, 1–57.

Saiki, R.K., 1990. Amplification of genomic DNA. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J. (Eds.), PCR Protocols. A Guide to Methods and Applications. Academic Press, San Diego, California, pp. 13–20.

Sorenson, M.D., 1996. TreeRot. University of Michigan, Ann Arbor, MI.

Starks, E.C., 1898. The osteology and relationships of the family Zeidae. Proc. U. S. Nat. Mus. 21, 469–476.

Stiassny, M.L.J., 1986. The limits and relationships of the acanthomorph fishes. J. Zool. London B 1, 411–460.

Stiassny, M.L.J., 1993. What are grey mullets? Bull. Mar. Sci. 52, 197–219.

Stiassny, M.L.J., Moore, J.A., 1992. A review of the pelvic girdle of acanthomorph fishes, with comments on hypotheses of acanthomorph interrelationships. Zool. J. Linnean Soc. London 104, 209–242.

Swofford, D.L., 1993. PAUP: Phylogenetic Analysis Using Parsimony. Illinois Nat. Hist. Survey, Champaign, IL.

Tang, K.L., Berendzen, P.B., Wiley, E.O., Morrissey, J.F., Winterbottom, R., Johnson, G.D., 1999. The phylogenetic relationships of the suborder Acanthuroidei (Teleostei: Perciformes) based on molecular and morphological evidence. Mol. Phylogenetics Evol. 11, 415–425.

Van der Peer, Y.I., Van den Broeck, De Rijk, P., de Wachter, R., 1994. Data base on the structure of small subunit RNA. Nucl. Acids. Res. 22 (17), 3488–3494.

Wheeler, W., Gladstein, D., 1994. MALIGN 1.99. American Museum of Natrual History, New York.

Wiley, E.O., 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. Wiley-Interscience, New York, 439pp.

Wiley, E.O., Johnson, G.D., Dimmick, W.W., 1998. The phylogenetic relationships of lampridiform fishes (Lampridiformes, Acanthomorpha), based on a total evidence analysis of Morphological and Molecular data. Mol. Phylogenetics Evol. 10 (3), 417–425.