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Phylogenetic Analysis of Veneridae (Bivalvia): Comparison of Molecular and Palaeontological Data

A. Canapa,¹ I. Marota,² F. Rollo,² E. Olmo¹

¹ Istituto di Biologia e Genetica, Facoltà di Scienze, Università di Ancona, via Brecce Bianche, I-60131 Ancona, Italy ² Dipartimento di Biologia Molecolare, Cellulare e Animale, Università di Camerino, I-62032 Camerino, Italy

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Abstract. An approximately 400-bp-long portion of the 16s rRNA gene sequence has been determined for the venerid clams Chamelea gallina (Chioninae), Dosinia lupinus (Dosiniinae), Pitar rudis, Callista chione (Pitarinae), Tapes decussatus, T. philippinarum, Venerupis (= Paphia) aurea (Tapetinae), and Venus verrucosa (Venerinae). Neighbor-joining and maximum parsimony trees support the results of traditional classification methods at the subfamily level but do not support the concept of a genus Tapes. The transversion divergence rate estimated on the basis of the palaeontological record for the C. gallina/V. verrucosa separation and for the Pitarinae is very close (0.14-0.16% per Myr, respectively) to that of ungulates and cetaceans, while the Tapetinae exhibit a much higher (0.36% per Myr) rate.

Key words: Veneridae — Bivalvia — mtDNA — Molecular clock — 16s rDNA

The Veneridae is a large and diverse family of Bivalvia, including more than 500 living species, that are classified into approximately 12 subfamilies, with 50 extant and 55 extinct genera. The members of this family live in various marine ecosystems and are characterized by having three cardinal teeth in each valve, and sometimes up to three anterior teeth. Valves show concentric sculpture ranging from smooth to pronounced, and sometimes radial and divaricate sculptures as well.

Venerid taxonomy is controversial and several dis-

crepancies among different systematic papers have been observed (Keen 1969; Fisher-Piette and Vukadinovic 1977). Mechanisms of adaptation to different environments and lifestyles may have strongly influenced the evolution of Veneridae, leading to several cases of parallelism in conchological characters of distantly related species and to extensive conchological diversification between closely related species (Harte 1992).

Recently, methodological approaches such as enzyme electrophoresis (Borsa et al. 1992), karyological analysis (Borsa and Thiriot-Quiévreux 1990; Insua and Thiriot-Quiévreux 1992), radio-immunoassay (Harte 1992), and highly repetitive DNA analysis (Passamonti et al. 1994; Canapa et al. 1993), have been used to study the taxonomy of Veneridae. Although most of these studies are limited to Tapetinae the results obtained have provided interesting contributions to clarifying some controversial aspects of venerid taxonomy. Moreover, they have confirmed that the systematics of this clam family, based only on morphological characters, may be influenced by evolutionary convergence phenomena.

Where morphological or physiological evidence of systematic relationships is unclear, genetic characters may provide accurate and unambiguous indicators of taxonomic divergence (Wilson et al. 1985). The mitochondrial gene for 16s ribosomal RNA has proved a powerful tool in phylogenetic studies and has provided information on the systematics of terrestrial and marine vertebrates (Allard et al. 1992; Milinkovitch et al. 1993) and on the systematics of marine invertebrates (Cunningham et al. 1992; Geller et al. 1993; Rumbak et al. 1994; Bucklin et al. 1995). To verify if this approach can con-

Correspondence to: E. Olmo

				10	20	30	40	50	
(ch			1	TTAACGGCCG	A AGT-TO	TCCIEGGEA	AGGTAGCATA	ATGATTAGCT	50
c.cn						ACTTCTCCTA	ACCTACCC	ATAA ATTCTC	50
C.ga			T	TTAACGGCTG	CAACGAG	AGTIGIGCIA	AGGTAGCGIG	ATAASITGIC	50
C.gi			1	AAACCGGCCG	CCCTAGCGTG	AGG-GTGCIA	AGGIAGCGAA	ATTCCTTGCC	50
D.lu			1	TTAACGGCTG	C – – – A A TGA G	ATTGTACTA	AGGTAGCG	ATAA G TTGTC	50
D mu			1	TTAACGGCT	TT-AA	TT TACTA	ARGTAGCGCG	GTAATTTACC	50
u				TAACGGCT		ACTTCTACTA	ACCTACCCC	ATAATTTCTC	50
T.de	19		1	TAACGGCIG	CAACGAG	AGIIGIACIA	AGGTAGCGCG	ATAATTIGIC	50
T.de	50		1	TAAACGGCTG	CAACGAG	AGTTGTACTA	AGGTAGCGCG	ATAATIIGIC	50
Tnh			1	TAATGGCTG	CAACGAG	AGTIGIACIA	AGGTAGCGCG	ATAATTTGTC	50
, p.,				TAAACCCCTC	C AACCEC	ΛΟΤΤΟΤΛΟΤΛ	ACCTACCCC	ATAATTTGTC	50
v.au			1	TAACGGCTG	CAACUGU	AUTTOTACTA			50
V.ve	20		1	ITAACGGCIG	CAACGAG	AGIIGIGCIA	AGGIAGCOLG	ATAASIIGIC	90
V.ve	21		1	TTAACGGCTG	C A A C G A G	A GTTGT GCTA	AGGTAGCGIG	ATAA G TTGTC	50
				60	70	80	90	100	
			- 4	00		CONTROLLE		TACTOTOT	100
C.ch			-51	CITTAATIGG	GOGANAGIAI	GAAIGGIIIG	ACGIGGAGA-	TACIGICITA	100
C.aa			51	TTTTAATTGG	AGAATGGTAT	GAATGGTTTA	ACGTAGAAT -	AACTGTCTTT	100
C ai			51	TTTTGATTGT	GGGCCTGCAT	GAATGGTTTA	ACGAGGGTTT	GACTGTCTCT	100
n 1			E1	TTTTAATTCA	ACAATCCTAT	CANTCOTTO	ATCICAAAA	ACCTATAT	100
D. LU			21	TTTTATTOA	AGAATOGTAT	DAATGGTTTG	A C C A C A A	ACTOTOTOT	100
P.ru			51	CITIAATIGG	GUGCIAUAA-	-AAIGGIIIG	ACGCAGAAA-	AACIGICIII	100
T.de	19		51	TTTTAATTGA	AGAATGGTAT	GAAAGGTCTG	TCGCAAGTI-	GCTIGICICI	100
T de	50		51	TTTTAATTG	AGAATGGTAT	GAAAGGTCTG	TCCCAAGTT-	GCTIGTCTCT	100
Tub	50		E1	TTTAATT	ACANTCOTAT	AAACCTTAC	ACCTOCOAT	TATTCTCTCT	100
1.pn			21	T CT TAATTAG	AGAATGGTAT	AAA GUUTTAU	ACGINGAT	CAUTCTCTCT	100
V.au			51	GIIAAIIGG	AGAAIGGIAI	GAA	ACGGAGALI	GALIGICIGI	100
V.ve	20		51	TTTTAATTGG	AGAATGGTAT	GAATGGTTTG	ACGTAGAAT -	GACTGTCTTT	100
V VA	21		51	ΤΤΤΤΔΑΤΤGG	AGAATGGTAT	GAATGGTTTG	ACGTAGAAT-	GACTGTCTTT	100
				110	1 7 0	120	140	150	
				110		150	140	1.20	
C.ch			101	ΑΑΤΑΤΑΑΤΑΑ	ATAGAAATTT	TITTTCAAGT	GAAAA AAC CT	GAAIIIIG-	150
C. aa			101	G GAAAA TAA -	AATTAAGTTT	CCATGTAAGT	GAAAAGGCTT	ATATTTTGT	150
C			101		ATTCAATTC	TACTCAACGT	GAA BATAC CT	TCATTER-AA	150
C.gr			101	ATTICITY	ALL GAA TIT	COTTITANCE	CHAACCETT	ATATATTAT	150
D.lu			101	ATALAAGLI-	AIGAAGIII	CCITITAAGI	GEAAAGGCII	ATATATTAT	120
P.ru			101	GATGTAATAA	AT-GAAATTT	CITTTCAAGT	GAAAAAGCII	GAGIIIIG-	150
T de	19		101	GAAAAAG AA -	AGCGAAGTTT	CCTTTTAAAT	GAAAAGGITT	AAGTAAA-GA	150
Tdo	50		101	CAAAACAA	ACCAAGTTT	COTTETANC	GAAAAGGUTT	AAGTAAA-GA	150
1.40	20		101	UAAAAA U JA	AGCOAAGTTT	COTTTTAA	MAAAAGGITT		150
T.ph			101	AAAAAAAIAL	AGHAAGHI	CCELETAAAL	AAAAGGIIII	AAALU-U-AU	120
V.au			101	AGAAAAGAA-	AATGAAGTTT	CCTTTTAAAT	GAAAAGGUTT	AAATIGI-AA	150
V ve	20		101	G GAAAATTA -	AACTAAGITI	CCTTTTAAGT	GAAAAGGCTT	ATATTTTGT	150
V vo	21		101	CONNALTA	AACTAACTT	COTTTANCT	GAAAAGGCTT	ATATTTTGT	150
v.ve	21		TOT		AACTAAGTTT	CCITITANGI	GRAMAGOCIT		100
				•				200	
				160	170	180	190	200	
C.ch			151	TAAAAGAAGA	GAAGACCCT	TCGA CTGAA	TTAGAAA	GT	200
6 00			151		GAAGACCCTG	ΤΓΓΑΛ	TTAA	AATTGITTGT	200
c.yu			131		A A CACCCTO	TCCATCT	THEAN	AATTAACTET	200
C.gi			121	AGTTAGACAA	AAAGACCCCG	I SCA AC		AATTACCT	200
D.lu			151	-AAAAGACGA	GAAGACCCIG	ICGAGIIIAA	A G	ATTIAATTAG	200
P.ru			151	TAITAGACGA	GAAGACCCT	TTGAACTTGA	TTACTGA	GTATAACTAT	200
Tdo	19		151	TAAAAGACGA	GAAGACCCT	TIGAGCITAA	TCAGGTTTTA	AATTITATEC	200
T	E0		151	ΤΛΛΛΛΟΛΟΟΑ	CANCACCCT	TTCACCTTAA	TCACCTUTTA	AATTITATCT	200
1.ae	50		121	TAAAAGACGA	GAAGACCCTA	TCCACCTTAA	TTAATTAA		200
T.ph			151	IAAAAGACGA	GAAGACCCIG	ICGAGCIIAA	ITAAATAAAA	AACHAGAHAH	200
V.au			151	TAAAAGACGA	GAAGACCCTG	CGAGCTTAA	TTAGGTTTAA	GAA	200
VVA	20		151	CAAAAGACGA	GAAGACCCTG	TCGAGCTTAA	TTAA	AATTATTTGT	200
1.16	20		151		CAACACCCTC	TCCACCTTAA		AATTATTCT	200
v.ve	21		121		GAAGACCCTG	TCOAOCITAA		AATIATIU	200
				210	220	Z30		250	_
C.ch			201	-TAAT	AATTGAAA	GTCAG	-TTA-TTATT	CTITIGA	250
6 00			201	TTATAT_			ΔGΔΔ		250
c.gu			201	NUTC N	CARCELA DA D		THINGCIECO	CCCC	250
c.gi			201		O GAO HAAAA		1114001000		2.50
D.lu			201	ASALIA			I AAA	A	250
P.ru			201	ATATTATAA	AGAATUATAA	ATTAGGTG	TTTAGTTATA	1111AGAA	250
T de	19		201	G	TGGTTA	TTATTIAA		AACT-	250
T 1.	E0		201	č	TCATTA			AACT	250
i.ae	50		201		A DOT OT	THAT THAT		THE TANK TO T	250
T.ph			201	GGIIAAAIGA	AAAJUGUUAA	I A G I T I AA I	GIIGGUIGAG		250
V.au			201		GAAAAA	TAGGCTAA		A-CT-	250
VVA	20		201	тігісл		TAA TT	AGAA	11111G	250
	21		201	TITICA		TALT	ACAA		250
11									200

Fig. 1. Alignment of 16s rDNA sequences of *C. chione* (C.ch), *C. gallina* (C.ga), *C. gigas* (C.gi), *D. lupinus* (D.lu), *P. rudis* (P.ru), *T. decussatus* (T.de), *T. philippinarum* (T.ph), *V. aurea* (V.au), *V. verrucosa* (V.ve). The specimens C.ch, C.ga, D.lu, P.ru, and V.au were collected along the coast near Ancona (Italy), V.ve specimens come from the Maliston Gulf near Split (Croatia); the T.de specimens come from the Gulf of Naples (Italy) and T.ph specimens were collected along the coast near Goro (Ferrara, Italy). Semipurified mitochondrial DNA was prepared according to Geller et al. (1993). One-half gram of clam foot is homogenized in 2 ml TEK (50 mM Tris-HCl pH 8.0, 10 mM EDTA, 1.5% NaCl). The homogenate is then centrifuged at 1,000g for 20 min and the supernatant is collected, diluted with 2 vol TEK, and finally centrifuged at 18,000g for 30 min at 4°C. The mitochondrial pellet is resuspended in 0.5 ml TEK and, following treatment with 0.5%

Nonidet P-40 at 0°C, extracted by 1 vol of phenol-chloroform. Eventually, the DNA is precipitated by ethanol. Semipurified mitochondrial DNA was PCR amplified using the universal 16AR (5'-CGCCTGTTTAACAAAAACAT-3') and 16BR (5'-CCGGTTTGAACTCAGATCACGT-3') oligonucleotide primers (Palumbi et al. 1991) under the following reaction conditions: 94°C, 1 min; 55°C, 30 s; 72°C, 1 min. Amplified DNA was directly sequenced in both senses using a manual procedure employing Taq polymerase ("Cycle Sequencing") and ³³P as the radioactive label. The alignment was performed using the Higgins-Sharp algorithm (CLUSTAL4) contained in the MacDNASIS (Hitachi) package, set at the default parameters. The voucher specimens are lodged in the Museum of the Faculty of Sciences of Ancona University.

			260	270	280	290	300	
C.ch		251		TGGGGTAACA	ATGGACTCAA	TAGAGCGTC-	TETTATIAT	300
C		251	······································	TCCCCAATA	TANATC AA	AATAACCCTT	TAATAACTAC	300
C.ga		251		IGGGGCAATA		AATAACGGIT	TAATAACTAG	200
C.gi		251	GAAAGCAAGI	CIAACC	<u>C</u> <u>G</u> A	-ATAACIAAC		300
D.lu		251	1	TGGGGGCAATA	-TAGGTT-AA	TTTA GC CATC.	HATCAATAAG	300
P.ru		251	ACTITUTG	TGGGGAAAGA	GAGGATTAAA	ACTAACATCC	ICTUATT-T	300
T do	10	251	AAAGTGTGCT	TECCEANAGE	TAGATTTAA	GA VAACAA GT	CTATATAGG	300
1.ue	19	251	AAAGTGTGGT	TCCCCLACC	TACATTTAA	CANAGAACT	CTATAATACC	200
I.ae	50	251	AAAGIGIGG	IGGGGAAAGC	-TAGATTIAA	GAAAACAAGI		200
T.ph		251	GAAGTUTAGT	T G G G G A G A G C	- I GAGIIIAA	GGIAATAAAC	ΙΑΑGΑΑΑΙΑ	300
V.au		251	GAAG <mark>G</mark> GTAGT	TGGGGA <mark>G</mark> AGC	-TAAACTTTA	GA GAATAA GT	TT-TGGGAGA	300
V Ve	20	251		TGGGGGAANA	-TAGACC-AA	AATAAC GGTT	TAATTATITA	300
V V	21	251		TCCCCCANTA	TACACC-AA	AATAACCCTT	ΤΛΛΤΤΛΤΓΤΛ	300
v.ve	21	271	u	TOOOOCAATA				
					· · · · · · · · · · · · · · · · · · ·			
			310	320	330	340	350	
C.ch		301	ATAA GAATCC	TATTT-GATA	G GAAA – GA T C	AAGAGITACC	GTAGGGATAA	350
6 00		301	ATAAAGATCC	TTECTCOANA	GAAAATAGC	AAAACGTACC	GCAGGGATAA	350
c.gu		201		CANTANATTC	CATCATAC	A ZA A CINTA CE	CCCCATAA	350
C.gi		201	III GAGCC	GADIALATIC	GAT CATA 56-	ASAAGITACS	CC DOODATAA	250
D.lu		301	G TA <u>G</u> AGATCC	TITAA-GAGA	GAAGAGAC	AAAA	GCAGGGATAA	350
P.ru		301	A TA GA GA GC C	TTTACAGAGA	GTCTA-AAGC	AAAAGITACC	ATAGGGATAA	: 350
T do	19	301	C-GAAGATCC	TCC-TCGGGA	GATAGTIGGT	AAAAGCTACC	GTAGGGATAA	350
TJ	F 0	201	C CAACATCC		CATAATTCCT	ΛΛΛΛΟΟΤΛΟΟ	CIACCATAA	350
1.ae	20	201	C-GAAGATCC	TCC-TCGGGA	GALAATIOGI	AAAAGCTACC	GAGGGATAA	350
T.ph		301	CTAAAGATCC	ICI-IIGAGA	GA - A GILAGC	AAAAGCIACC	GCAGGGATAA	350
V.au		301	C-AGAGATCC	TCT-CGGAGA	GA – AATAGGT	AAAAGCTACC	GCAGGGATAA	350
VVA	20	301	ΔΤΔΔΔGΔΤCC	TTTGTTGATA	GAAAAT AGC	AAAAGCTACC	GCAGGGATAA	350
V.VC	21	201	ΑΤΑΑΑGATCC	TTTCTTCA	CAAAAT ACC	ΛΛΛΛΟΓΤΛΟΟ	GENGGGATAA	350
v.ve	21	201	ATAAAGATCC	TTTUTTUANA	UAAAA I AAUC	MARAOCIACC	OCAUUUATAA	550
						200	400	
			260	470		4UIA	400	
					500	590		
C.ch		351	CAGCCTAATA	TCTTTCTGAG	AGGICTTATT	GAGGG GAGGG	TGTGCGACCT	400
C.ch C.aa		351 351	CAGCCTAATA	TCTTTCT GAG	AGGICTTATT AGATC GA ATT	GAGGG <mark>G</mark> AGGG GAG G GAGGG	TGTGCGACCT TTTGCGACCT	400 400
C.ch C.ga		351 351 351			AGGICTTATT AGATCGAATT	GAGGG <mark>G</mark> AGGG GAG <mark>A</mark> GAAGGG	TGTGCGACCT TTTGCGACCT	400 400 400
C.ch C.ga C.gi		351 351 351		TCTTTCTGAG CCTTCTTAAG CTTTAGIAG	AGGICTTATT AGATCGAATT AGTICGIATT	GAGGG <mark>G</mark> AGGG GAGAGAGGG G GCTA AAGGG	TGTGCGACCT TTTGCGACCT ATTGGCACCT	400 400 400
C.ch C.ga C.gi D.lu		351 351 351 351	CAGC CTAATA CAGCGT AT CAG CGT AATC CAGCGT AATC	TCTTTCIGAG CCTTCTTAAG CIITTAGI-AG CCTTTTTAAG	AG <mark>G</mark> ICTTATT AGATC <mark>GA</mark> ATT AG T CGTATT AGATCTTATT	GAGGG <mark>G</mark> AGGG GAGAGGG G GCTA AAGGG GAGAGAAGGG	TGTGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT	400 400 400 400
C.ch C.ga C.gi D.lu P.ru		351 351 351 351 351 351	CAGC GTAATA CAGCGT TAAT- CAG GC TAATC CAGCGT TAT- CAGCGT ATT	TCTTTCTGAG CCTTCTTAAG CTTTTAG CCTTTTTAAG CCTTTTTAAG CCTTTTTAAG	AGGICTTATT AGATCGAATT AGIICGIATT AGATCTTATT AGATCTTATT AGCICTTATT	GAGGG <mark>G</mark> AGGG GAGAGAGGG G GCTA AAGGG GAGAGAAGGG GAGG <mark>AG</mark> AGGG	TGTGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de	19	351 351 351 351 351 351 351	CAGC CTAATA CAGC GT TAT CAG CGT TAT CAGC GT TAT CAGC GT AAT CAGC GT AAT	TCTTTCTGAG CCTTCTTAAG CTTTAGI-AG CCTTTTAAG CCTTTTAAG CCTTTTGAG	AGGICTTATT AGATCGAATT AGTCGIATT AGATCTTATT AGATCTTATT AGATCTTATT	GAGGGGGAGGG GAGAGAGGG GCTAAAGGG GAGAGAGGG GAGGAGAGGG GAGGAGAAGGG	TGTGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400
C.ch C.ga D.lu P.ru T.de	19 50	351 351 351 351 351 351 351 351	CAGCGTAATA CAGCGTTAT- CAGGCTAATC CAGCGTAATT CAGCGTAATT CAGCGTAAT- CAGCGTAAT-	TCTTTCTGAG CCTTCTTAAG CTTCTTAAG CTTTTAG CCTTTTAAG CCTTTTAAG CCTTTTAAG CTTTTTAAG	AGGICTTATT AGATCGAATT AGTICGIATT AGATCTATT AGATCTTATT AGATCTTATT AGATCTTATT	GAGGG GAGG GAGAGGG GGCTAAGGG GAGAGGG GAGGAGAGGG GAGGGAAGGG GAGGGAAGGG	TGTGCGACCT TTTGCGACCT ATTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400
C.ch C.ga D.lu P.ru T.de T.de	19 50	351 351 351 351 351 351 351 351	CAGC GTAATA CAGC GT IIAT CAG GC TIIAT CAGCGT IIAT CAGCGTAATT CAGCGTAAT CAGCGTAAT	TCTTTCTGAG CCTTCTTAAG CTTTTAGI AG CCTTTTTAAG CCTTTTTAAG CCTTTTTAAG CTTTCTTGAG CTTTCTTGAG	AGGICTTATT AGATCGAATT AGATCGIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT	GAGGGGAAGGG GAGAGGG GGTAAGGG GAGAGAGGG GAGGAGAGG GAGGGAAAGG GAGGGAAAGG GAGGGAAAGG	TIGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.de	19 50	351 351 351 351 351 351 351 351	CAGC GTAATA CAGC GT TAT CAGC GT TAT CAGC GT TAT CAGC GTAAT CAGC GTAAT CAGC GTAAT CAGC GTAAT	TCTTTCI GAG CCTCTTAAG CTTCTTAAG CTTTAGI AG CCTTTTAAG CCTTTTAAG CTTTTAAG CTTTTAAG CTTCTTAAG CTTCTTAAG	AG GICTTATT AGATC GAATT AG IIC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT	GAGGGGAGGG GAGGGGAAGGG GAGAGAGGG GAGGAGAGGG GAGGAAGGG GAGGGAAAGG GAGGGAAAGG GAGGGAAAGG	TIGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.ph V.au	19 50	351 351 351 351 351 351 351 351 351	CAGCGTAATA CAGCGTTAATC CAGCGTTAATC CAGCGTTAATC CAGCGTAAT CAGCGTAATC CAGCGTAATC CAGCGTAATC	TCTTTCI GAG CCTTCTTAAG CCTTTTAG CCTTUTAG CCTTUTAAG CCTTUTGAG CUTTCTTGAG CUTTCTTGAG TCTTUTAAG TTTGCTTGAG	AG GICTTATT AGATC GAATT AGUIC GIATT AGATCTTATT AG GICTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT	GAGGGGAAGGG GAGAGGG G GCTA AAGGG GAGAGAAGGG GAGGAAAGGG GAGGGAAAGG GAGGGAAAGG GAGGGAAAGG GAGGGAAAGG GAGGGAAGG	TIGCGACCT TTGCGACCT ATTGGCACCT TTGCGACCT TTGCGACCT TTGCGACCT TTGCGACCT TTGCGACCT	400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.ph V.au V.ve	19 50 20	351 351 351 351 351 351 351 351 351	CAGC GTAAT CAGC GT IAT CAG GC TAAT C CAGC GT IAT CAGC GTAAT CAGC GTAAT CAGC GTAAT CAGC GTAAT CAGC GTAAT CAGC GTAAT CAGC GTAAT	TCTTTCI GAG CCTCTTAAG CTTCTTAAG CTTCTTAAG CCTTTTAAG CCTTTTAAG CTTTTTAAG CTTCTTGAG TCTTTTAAG CCTTCTTAAG CCTTCTTAAG	AG GICTTATT AGATC GAATT AG TC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT	GAGGG GAGGG GAGAGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGGAAAGG GAGGGAAAGG GAGGGAAAGG GAGGGAAGAG GAGGGAAGAG GAGGGAAGGG	TGIGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.ph V.au V.ve V.ve	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGC GTAATA CAGC GT TAT CAG GC TAATC CAGC GT TAT CAGC GTAAT CAGC GTAAT CAGC GTAAT CAGC GTAAT CAGC GT TAT CAGC GT TAT CAGC GT TAT		AG GICTTATT AGATC GAATT AG TC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATC GAATT AGATC GAATT	GAGGGGAAGGG GAGAGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGAAAGGG GAGGGAAAGG GAGGGAAAGG GAGGGAAGAG GAGGGAAGGG GAGGGAAGGG	TIGCGACCT ATTGCGACCT ATTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.ph V.au V.ve V.ve	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGC GT IAT CAGC GT IAT CAGC GT IAT CAGC GT IAT CAGC GT AAT CAGC GT AAT CAGC GT AAT CAGC GT AAT CAGC GT AAT CAGC GT IAT CAGC GT IAT		AG GICTTATT AGATC GAATT AG TC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTATT AGATC GAATT AGATC GAATT	GAGGGGAAGGG GAGAGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGAAGAGGG GAGGGAAAGG GAGGGAAAGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG	TIGCGACCT ATTGCGACCT ATTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.ph V.au V.ve V.ve	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGCCTAATA CAGCGTTAT- CAGCGTTAT- CAGCGTAATC CAGCGTAAT- CAGCGTAAT- CAGCGTAAT- CAGCGTAAT- CAGCGTAAT- CAGCGTAAT- CAGCGTTAT- CAGCGTTAT-		AG GICTTATT AGATC GAATT AG IC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTATT AGATCTATT AGATCGAATT AGATCGAATT AGATCGAATT	GAGGGGAAGGG GAGGGGAAGGG GAGAGAGGG GAGGAG	TIGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.de V.ve V.ve V.ve	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGCGTIAT CAGCGTIAT CAGCGTIAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTIAT CAGCGTIAT		AG GICTTATT AGATC GAATT AG TIC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATC GAATT AGATC GAATT AGATC GAATT	GAGGG GAGGG GAGAGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGAAAGG GAGGGAAAGG GAGGGAAAGG GAGGGAAGAG GAGGGAAGAG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG	TGIGCGACCT TTGCGACCT ATTGGCACCT TTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.ph V.au V.ve V.ve C.ch	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGCGTTAT CAGCGTTAT CAGCGTTAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTTAT CAGCGTTAT CAGCGTTAT CAGCGTTAT		AG GICTTATT AGATC GAATT AG TC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATC GAATT AGATC GAATT AGATC GAATT 430	GAGGG GAGGG GAGAGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGAAAGGG GAGGGAAAGG GAGGGAAAGG GAGGGAAGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG	TGTGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.ph V.au V.ve V.ve C.ch C.ga	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGCGT TAT CAGCGT TAT CAGCGT TAT CAGCGT TAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTTAT CAGCGT TAT CAGCGT TAT CAGCGT TAT		AG GICTTATT AGATC GAATT AG TC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTATT AGATCTATT AGATC GAATT AGATC GAATT 430	GAGGG GAAGGG GAGGGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGAAGGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG 440	TGIGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.ph V.au V.ve V.ve C.ch C.ga C.gi	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGCGTIAT CAGCGTIAT CAGCGTIAT CAGCGTAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTIAT CAGCGTIAT CAGCGTIAT CAGCGTIAT CAGCGTIAT		AG GICTTATT AGATC GAATT AGGIC GIATT AGGICTTATT AGGTCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTATT AGATC GAATT 4GATC GAATT 430	GAGGG GAGGG GAGAGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGAAAGGG GAGGGAAAGG GAGGGAAGAGG GAGGGAAGAGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG 440	TGIGCGACCT TTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT 450	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.ph V.au V.ve V.ve C.ch C.ga C.gi D.lu	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGC GT TAT CAGC GT TAT CAG CGT TAT CAGC GT AAT C CAGC GT AAT CAGC GT AAT CAGC GT AAT CAGC GT AAT CAGC GT AAT CAGC GT TAT CAGC GT TAT CAGC GT TAT CAGC GT TAT CAGC GT TAT CAGC GT TG GA CGAT GT TG GA CGAT GT TG GA	ТСТТІСІ ДА ССТСТТАА СТТСТТАА СТТСТТАА СТТТІТАА СТТІТАА СТТІТАА СТТІТАА СТТСТТАА СТТСТТАА СТТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТСТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТСТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТСТАА ССТСТСТАА ССТСТСТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТСТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТСТТАА ССТСТСТТАА ССТСТТАА ССТСТТАА ССТСТСТТАА	AG GICTTATT AGATC GAATT AG TC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCGAATT AGATCGAATT 430	GAGGG GAGGG GAGAGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGGAAAGG GAGGGAAAGG GAGGGAAAGG GAGGGAAGAG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG 440	TGTGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT 450	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.ph V.ve V.ve V.ve C.ch C.ga C.gi D.lu	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGCGTTAT CAGCGTTAT CAGCGTTAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTTAT CAGCGTTAT CAGCGTTAT CAGCGTTAT CAGCGTTGA CGATGTTGGA CGATGTTGGA CGATGTTGGA		AG GICTTATT AGATC GAATT AG TC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTATT AGATCTATT AGATC GAATT AGATC GAATT 430	GAGGGGAAGGG GAGAGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGAAGGG GAGGGAAAGG GAGGGAAAGG GAGGGAAGAG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG AAGGGAAGGG 440	TGTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT 450	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.ph V.au V.ve V.ve C.ch C.ga D.lu P.ru	19 50 20 21	351 351 351 351 351 351 351 351 351 351	CAGCCTIAT CAGCCTIAT CAGCGTIAT CAGCGTAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTAAT CAGCGTTAT CAGCGTTAT CAGCGTTAT CAGCGTTGA CGATGTTGGA CGATGTTGA	ТСТТТСІ БА ССТТСТТАА СПТТАБІ А ССТТСТТАА СПТТАБІ А ССТТПТАА СПТТТТАА СПТТСТТБА ПТТТТБА ТСТТПТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТТАА ССТСТАА ССТСТТАА ССТСТАА ССТСТТАА ССТСТТАА ССТСТАА ССТСТТАА ССТСТАА ССТСТАА ССТСТАА ССТСТАА ССТСТАА ССТСТАА ССТСТАА ССТСТАА ССТСТАА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССТСА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССА ССССС	AG GICTTATT AGATC GAATT AG TC GIATT AG TC GIATT AG TCTTATT AG ATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTATT AGATC GAATT 430	GAGGG GAGGG GAGAGAAGGG GAGAGAAGGG GAGAGAAGGG GAGGAAAGGG GAGGGAAAGG GAGGGAAAGG GAGGGAAGAGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG GAGGGAAGGG 440	TGIGCGACCT TTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT 450	400 400 400 400 400 400 400 400 400 400
C.ch C.ga C.gi D.lu P.ru T.de T.de T.de V.au V.ve V.ve C.ch C.ga C.gi D.lu P.ru T.de T.ph V.au V.ve	19 50 20 21	351 351 351 351 351 351 351 351 351 351		ТСТТІСІ ДА ССТСТТАА СТТСТТАА СТТСТТАА СТТСТТАА СТТІТАА СТТІТАА СТТІТАА СТТСТІ ДА СТТСТІ ДА СТТСТІ ДА СТТСТІ ДА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТСТТАА ССТТСТТАА ССТТСТТАА ССТТСТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТССТТАА ССТ	AG GICTTATT AGATC GAATT AG TC GIATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTTATT AGATCTATT AGATCGAATT 4GATC GAATT 430	GA GG G GA GG G GA GA GA A GG G GA GA GA A GG G GA GA GA A GG G GA GG GA A GG G GA GG GA A A GG GA GG GA A GG G GA GG GA A GG G 440	TGTGCGACCT TTTGCGACCT ATTGGCACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT TTTGCGACCT A50	400 400 400 400 400 400 400 400 400 400
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Fig. 1. Continued.

tribute to clarify the systematics and phylogeny of Veneridae, we have determined the nucleotide sequence of an approximately 400-bp-long portion of the 16s rRNA gene in Chamelea gallina (Linné, 1758) (Chioninae), Dosinia lupinus (Linné, 1758) (Dosiniinae), Venus verrucosa (Linné, 1758) (Venerinae), Tapes decussatus (Linné, 1758), T. philippinarum (Adams & Reeve, 1850) (usually assigned to *Ruditapes*), *Venerupis* (= *Paphia*) aurea (Gmelin, 1791) (Tapetinae), Pitar rudis (Poli, 1795), and Callista chione (Linné, 1758) (Chioninae). Chione, gallina, verrucosa, and decussatus are, respectively, the type species of the genera Callista, Chamelea, Venus, and Tapes (Ruditapes). The sequences have been used to construct phylogenetic trees (utilizing different methods) and the results have been compared with the palaeontological data.

Sequences of the 16s rRNA gene fragment (not including the primer sequence) from the above-mentioned species and from *Crassostrea gigas* (Ostreida:Bivalvia), are shown in Fig. 1. In the case of *T. philippinarum*, *T. decussatus*, and *V. verrucosa*, two specimens for each species were analyzed. The two *T. philippinarum* specimens showed identical sequences, while a single basepair insertion/deletion distinguishes the two *V. verrucosa*. The largest difference (five transitions) was observed in the case of *T. decussatus*.

Phenetic analysis of the sequence data for each pair of taxa is presented in Table 1. In general, the number of pairwise substitutions is rather high, ranging from approximately 15% (between *V. aurea* and *T. philippina-rum*) to 42.% (between *D. lupinus* and *C. gigas* and between *C. gigas* and *T. decussatus*). An exception is

	C.ch	C.ga	C.gi	D.lu	P.ru	T.d19	T.d50	T.ph	V.au	V.v20	V.v21
C.ch	0	1.2	0.6	1.4	1.3	1.4	1.4	1.3	1.6	1.3	1.3
C.ga	28.6	0	0.7	1.2	1.2	1.3	1.3	1.4	1.2	1.6	1.6
C.gi	39.4	38.9	0	1.0	0.7	1.0	1.0	0.9	1.0	0.8	0.8
D.lu	30.5	18.7	42.6	0	1.3	1.5	1.3	1.2	1.5	1.3	1.3
P.ru	23.2	30.0	41.2	29.7	0	1.2	1.2	1.2	1.4	1.3	1.2
T.d19	35.3	22.5	42.4	24.6	33.3	0	_ ^a	2.3	2.7	1.3	1.3
T.d50	35.3	22.0	41.5	24.3	32.5	1.3	0	2.3	2.9	1.3	1.3
T.ph	33.0	21.6	41.4	22.5	33.3	20.2	20.2	0	1.7	2.0	1.8
V.au	32.3	20.8	38.3	23.3	32.8	16.4	15.8	15.3	0	1.3	1.2
V.v20	26.7	6.3	37.6	18.7	28.5	21.9	21.3	19.6	20.2	0	_ ^b
V.v21	26.5	6.3	37.4	18.7	28.3	21.7	21.1	19.4	19.9	0.0	0

Table 1. Pairwise distance-matrix for the 16s ribosomal RNA gene fragment. Below diagonal, percent difference values; above diagonal, transition/transversion ratio (abbreviations as in Fig. 1)

^a 5 transitions/0 transversions

^b 0 transitions/0 transversions

represented by the genera Chamelea (Chioninae) and Venus (Venerinae), which show 6.3% base substitutions only. In contrast, the two species of the genus Tapes considered in this study (T. decussatus and T. philippinarum) show 20% sequence divergence, which is higher that between V. aurea and T. decussatus (approximately 16%) and V. aurea and T. philippinarum (approximately 15%). It may be worth mentioning that *T. decussatus* is a northeast Atlantic/Mediterranean species while T. philippinarum is a northwest Pacific species, each of which had been geographically isolated for a very long time before the latter was introduced into the Mediterranean recently. We have excluded from our analysis the central region of the examined sequences, because it appears very variable. However, very similar results were obtained when also including this region in the analysis.

In general, mitochondrial sequences from metazoans show a transition bias (Brown et al. 1982; Rumbak et al. 1994). A ratio of transitions to transversions of about ten indicates that the sequences are far from saturation. Once transitions have become saturated, the transversions continue to accumulate approximately linearly with time (Miyamoto and Boyle 1989). The data in Table 1 (above diagonal) exhibit transition/transversion rates very close to one, sometimes even lower than one, indicating that we are deep within the saturation zone.

According to Keen (1969), the Veneridae family probably is polyphyletic in origin; subfamily divisions do not necessarily reflect genetic relationships, but are adopted for convenience in arrangement. More recent studies, on the other hand, indicate that Veneridae have a monophyletic origin but are by far more deeply divided than shown by the morphological analyses (Harte 1992).

All the taxa considered in the present investigation show a similar (37-42%) divergence from *C. gigas*. Sequence divergence detectable within the Veneridae is constantly lower, though in the case of *T. decussatus* and *C. chione* (35% sequence divergence), not much lower. The even distance of all taxa from *C. gigas* may be attributable to transition saturation.

A phylogenetic tree calculated using neighbor-joining is shown in Fig. 2. We can observe that D. lupinus is basal to the Tapetinae. This early dicotomy, however, is only weakly supported (bootstrap value = 54). A maximum parsimony (branch and bound) tree (Swofford 1993) shows the same topology. If different methods of parsimony tree construction (e.g., heuristic search) are used, the dicotomy collapses to polytomy. All the trees are also consistent with the inclusion of T. decussatus, T. philippinarum, and V. aurea into one (Tapetinae) subfamily. Neither tree supports the concept of a genus Tapes as, in both cases, V. aurea clusters with T. decussatus. In contrast to the previous results, transversion analysis using neighbor-joining presents the phylogeny of the venerid subfamilies as essentially polytomic (Fig. 3). This tree confirms that the concept of a genus Tapes has no phylogenetic basis. In conclusion, our data strongly support the idea (Insua and Thiriot-Quiévreux 1992) that the Tapetinae form a heterogeneous group and T. decussatus and T. philippinarum are probably much more genetically distant than assumed so far on the basis of morphology.

Early members of the superfamily Veneracea are found in the Lower Cretaceous, i.e., they are about 100– 135 million years (Myr) old (Keen 1969). The fossil record, on the other hand, indicates a broad range of ages for the different genera considered in the present study (Table 2), with the oldest taxon represented by *Callista*, the youngest by *Venerupis*, while *Chamelea* and *Venus* are of intermediate age.

The transversion divergence rate for mitochondrial ribosomal genes of ungulates and cetaceans has been computed to be about 0.14% per Myr (Allard et al. 1992; Milinkowitch et al. 1993). If we apply this rate to the separation *C. gallina/P. rudis*, we obtain a figure (100 Myr) which fits very well with the indication of a Lower Cretacean origin of the Veneracea. However, previous reports have shown that animal mitochondrial DNA (mtDNA) can display variable rates of sequence evolution among taxa (Rand 1994). Different evolutionary



Fig. 2. Neighbor-joining (Saitou and Nei 1987) tree constructed with pairwise distances calculated following the application of Kimura's (1980) two-parameter correction for multiple substitutions. The tree was produced using TREECON (Van de Peer and De Wachter 1993). The *numbers* represent the percentage of 100 bootstrap replications in which a given node appeared. *Abbreviations* as in Fig. 1.



Fig. 3. Neighbor-joining (Saitou and Nei 1987) tree calculated on the basis of the sole transversions. The tree was produced using TREECON (Van de Peer and De Wachter 1993). The *numbers* represent the percentage of 100 bootstrap replications in which a given node appeared. *Abbreviations* as in Fig. 1.

 Table 2. The fossil record of the venerid species considered in the present study

Subfamily	Species	Oldest fossil record ^a
Chioninae	C. gallina	Oligocene (25–40 Myr ago)
Dosiniinae	D. lupinus	Miocene (11–25 Myr ago)
Pitarinae	Pitar sp.	Eocene (40-60 Myr ago)
	C. chione	Paleocene (60–70 Myr ago)
Tapetinae	Tapes sp.	Miocene (11–25 Myr ago)
-	T. decussatus	Miocene (11–25 Myr ago)
	Venerupis sp.	Pliocene (1–11 Myr ago)
Venerinae	V. verrucosa	Oligocene (25-40 Myr ago)

^a According to Keen (1969)

rates of "molecular clocks" are also found in the nuclear genes for ribosomal RNA of several Bivalvia (Rice et al. 1993). The transversion divergence rate computed for *Callista* and *Pitar* (0.16% per Myr) on the basis of the age of the first fossil record is not much different from

that of ungulates and cetaceans. A remarkably similar transversion divergence rate (0.14% per Myr) is also found if we consider the *V. verrucosa/C. gallina* separation. These figures, however, double if we consider *T. decussatus/V. aurea* and *T. decussatus/T. philippinarum* (0.31% and 0.36% per Myr, respectively).

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