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Karyotypes of *Cerastoderma edule*, *Venerupis pullastra* and *Venerupis rhomboides* (Bivalvia, Veneroida)

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Abstract

The chromosomes of three commercially important species of veneroid bivalves were studied: *Cerastoderma edule* (Cardiidae), *Venerupis pullastra* and *Venerupis rhomboides* (Veneridae, Tapetinae) using conventional Giemsa staining and morphometric measurements. *C. edule* showed a diploid chromosome number of $2n=38$ and a variable occurrence of supernumerary chromosomes. Its karyotype consists of 12 submetacentric, 4 subtelocentric and 3 telocentric chromosome pairs. The supernumerary chromosomes were easily distinguished by their reduced differentiated size and by their intra and inter-individual variability. *C. edule* is the first bivalve species where supernumerary chromosomes have been observed. *V. pullastra* had $2n=38$ with a karyotype including 3 metacentric, 8 submetacentric and 8 subtelocentric chromosome pairs. *V. rhomboides* had $2n=38$ with a karyotype including 4 metacentric, 8 submetacentric, 4 subtelocentric and 3 telocentric chromosome pairs. Cytotaxonomic relationships are proposed within Tapetinae from comparative analysis of karyotypes of two species studied here and three other species of the same subfamily previously studied.

Keywords : Chromosome, karyotype, bivalve, Cardiidae, Veneridae, Tapetinae.

Les caryotypes de Cerastoderma edule, Venerupis pullastra *and* Venerupis rhomboides (*Bivalvia, Veneroida*).

Résumé

Les chromosomes de trois espèces d'importance commerciale de Bivalves Vénéroidés, *Cerastoderma edule* (Cardiidae), *Venerupis pullastra* et *Venerupis rhomboides* (Veneridae, Tapetinae) ont été étudiés après coloration standard au Giemsa et mesures morphométriques. *C. edule* montre un nombre chromosomique diploïde de $2n=38$ et la présence de chromosomes surnuméraires. Son caryotype comprend 12 paires de chromosomes submétacentriques, 4 subtélocentriques et 3 télocentriques. Les chromosomes surnuméraires sont aisément différenciés par leur taille très réduite et leur variabilité intra et inter-individu. *C. edule* est la première espèce de Bivalve où ces structures ont été observées. *V. pullastra* a $2n=38$ avec un caryotype incluant 3 paires de chromosomes métacentriques, 8 submétacentriques and 8 subtélocentriques. *V. rhomboides* a $2n=38$ et son caryotype comprend 4 paires de chromosomes métacentriques, 8 submétacentriques, 4 subtélocentriques and 3 télocentriques. Des relations cytotaxonomiques sont proposées au sein des Tapetinae par l'analyse comparative des caryotypes des deux espèces étudiées dans ce travail et de trois autres espèces de la même sous-famille étudiées précédemment.

Mots-clés : Chromosome, caryotype, Bivalve, Cardiidae, Veneridae, Tapetinae.

INTRODUCTION

The Veneroida include two families, the Cardiidae and the Veneridae, with many species of commercial importance. Chromosome studies have previously been reported on four species of Cardiidae and 12 species of Veneridae: chromosome number (Menzel and Menzel, 1965; Menzel, 1968; Gérard, 1978; Rasotto *et al.*, 1981), chromosome number and morphology (Koulman and Wolff, 1977; Corni and Trentini, 1986; 1990), karyotype (Ieyama, 1980) and karyometric analysis (Ieyama, 1985; Borsa and Thiriot-Quiévreux, 1990). The characterization of karyotype by conventionally stained chromosomes and morphometric measurements of chromosomes is the first step used to describe the chromosomal features of a species. Afterwards, banding techniques can aid in elucidation and clarification of the fine characterization of the different chromosome pairs.

This report presents the karyotypes and morphometric measurements of chromosomes in one species of Cardiidae: *Cerastoderma edule* (Linné, 1758), and two species of Veneridae (subfamily Tapetinae): *Venerupis pullastra* (Montagu, 1803) and *Venerupis rhomboides* (Pennant, 1777).

MATERIAL AND METHODS

Specimens of *C. edule* and *V. pullastra* were intertidally collected at Baldayo (NW coast Iberian Peninsula). Specimens of *V. rhomboides* were dredged at 10 m depth at Ria de Arosa (NW coast Iberian Peninsula). The three populations studied were wild populations and sampled in December 1990. Before processing, the animals were reared in the laboratory for two weeks.

Whole juvenile animals were treated for 7 h with 0.005% colchicine in sea water. The gills were then dissected out and treated for 30 min in 50% diluted sea water, followed by 30 min in sea water diluted to 25%. Fixation involved three changes (20 min each) of a freshly prepared solution of absolute ethanol-acid acetic (3:1). In order to improve chromosome lengthening, some animals were incubated for 3 days in 5-bromodeoxyuridine (Brd U) at 50 µg/ml in sea water before treatment with colchicine and dissection. Each slide preparation was made from one individual using an air-drying technique (Thiriot-Quiévreux and Ayraud, 1982). Slides were then stained directly with Giemsa (4%, pH 6.8) for 10 min and photographs of well-spread metaphases were taken with a Zeiss III photomicroscope.

For karyotyping, chromosomes were cut out of the photomicrographs and paired on the basis of size and centromere position. Morphometric measurements of chromosomes in the karyotypes of 10 metaphasic cells in each species studied were made with a digitalizer table (Summa Sketch II) interfaced to a Macintosh Classic computer. Data analysis was performed using a macro program in Microsoft Excel. Relative length (Rl) was expressed as 100 times the absolute chromosome pair length (in µm) divided by the total length of the haploid complement. Centromeric index (Ci) was calculated by dividing 100 times the length of the short arm by the total chromosome length. The arm ratio (Ar) which expresses also the centromere position was determined (length of short arm divided by length of long arm). Means and standard deviation of Rl, Ci and Ar were calculated for each chromosome pair. Terminology relating to centromere position follows that of Levan *et al.* (1964). When a centromere position was found to be on the borderline between two categories, the confidence limit of the means of Ci was calculated $p=0.05$ and two chromosome categories are listed.

RESULTS

Cerastoderma edule

The chromosomes of 35 mitotic metaphases (see metaphases in *fig.* 1, A and B) taken from 14 animals were counted. 28 cells had $2n=38$, the remaining being aneuploid ($2n=35-37$). The presence of supernumerary chromosomes in addition to those of the standard complement was observed in 15 cells. They were easily distinguished by their reduced differentiated size, which is much smaller than that of the smallest in the standard complement (*fig.* 1, A and *fig.* 2, A) and their numerical variation (1 or 3). Both inter and intra-individual variations in supernumerary chromosome numbers were found. Means and SD of Rl, Ar and Ci and given in *table* 1. The karyotype (*fig.* 2, A) consists of 19 pairs with a regular decrease in size. Twelve pairs are submetacentric (pair 8, 15, 18 being submetacentric-subtelocentric and pair 16, submetacentric-metacentric), 4 pairs are subtelocentric and 3 are telocentric-subtelocentric (*fig.* 3).

Venerupis pullastra

The chromosomes of 93 mitotic metaphases (*fig.* 1, C) taken from 10 animals were counted. 67 cells had $2n=38$, the remaining being aneuploid ($2n=35$-37). Means and SD of Rl, Ar and Ci are given in *table* 2. The karyotype (*fig.* 2, B) consists of 3 metacentric, 8 submetacentric (pairs 3 and 10 being submetacentric-metacentric; pairs 11 and 18 submetacentric-subtelocentric) and 8 subtelocentric (pairs 12, 13, 17 being subtelocentric-submetacentric) (*fig.* 4). The metacentric pair 6 was characterized by the presence of a secondary construction in 36 of the cells analysed. Its occurrence appears either on the two

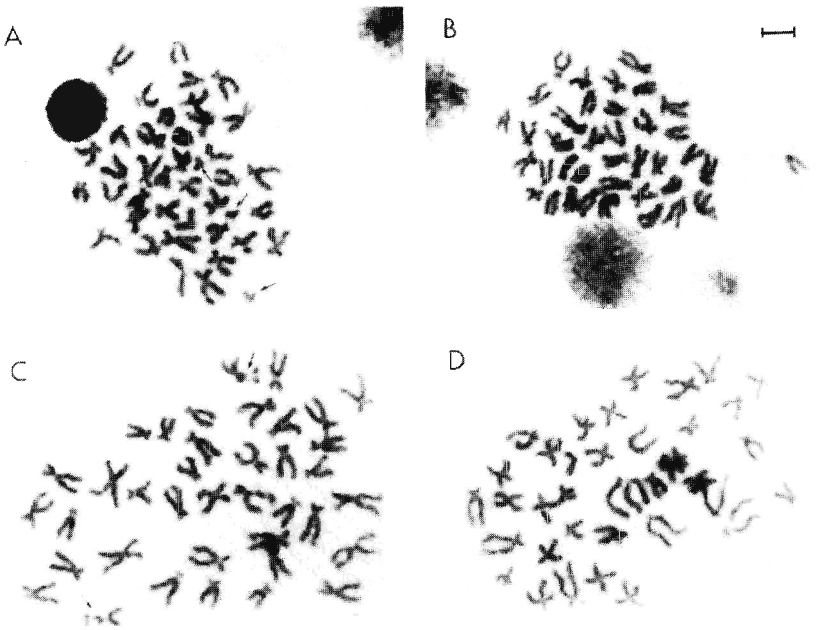

Figure 1. – Mitotic metaphases. A: *Cerastoderma edule*, note three supernumerary chromosomes (arrows); B: *C. edule*, metaphase without supernumerary chromosomes; C: *Venerupis pullastra*, note the secondary constrictions (arrows); D: *Venerupis rhomboides*. Scale bar = 5 μm.

Table 1. – Chromosome measurements and classification derived from ten metaphase cells of *Cerastoderma edule* (m: metacentric; sm: submetacentric; st: subtelocentric; t: telocentric).

Chromosome pair No.	Relative length		Arm ratio		Centromeric index		Classification
	Mean	SD	Mean	SD	Mean	SD	
1	7.169	0.454	0.533	0.088	34.418	3.633	sm
2	6.479	0.383	0.510	0.072	33.469	3.370	sm
3	6.329	0.356	0.460	0.088	31.150	4.199	sm
4	6.081	0.284	0.404	0.042	28.546	2.134	sm
5	5.849	0.282	0.286	0.037	22.025	2.201	st
6	5.543	0.437	0.457	0.075	30.987	3.689	sm
7	5.489	0.274	0.458	0.100	30.989	4.240	sm
8	5.398	0.307	0.357	0.064	26.090	3.349	sm-st
9	5.273	0.399	0.129	0.040	11.213	3.074	t-st
10	5.073	0.187	0.457	0.051	31.072	2.475	sm
11	4.908	0.258	0.385	0.074	27.469	3.745	sm
12	4.906	0.190	0.244	0.058	19.352	3.789	st
13	4.821	0.235	0.309	0.056	23.355	3.343	st
14	4.711	0.204	0.315	0.046	23.760	2.687	st
15	4.582	0.294	0.353	0.064	25.793	3.519	sm-st
16	4.565	0.233	0.603	0.081	37.199	3.348	sm-m
17	4.474	0.259	0.142	0.045	12.272	3.340	t-st
18	4.205	0.309	0.342	0.061	25.208	3.372	sm-st
19	4.145	0.541	0.162	0.116	12.368	5.424	t-st

homologous chromosomes or on one chromosome only.

Venerupis rhomboides

The chromosomes of 57 mitotic metaphases (*fig.* 1, D) taken from 15 animals were counted. 45 cells had $2n = 38$, the remaining being aneuploid ($2n = 35$-37). Means and SD of RI, Ar and Ci are given in *table* 3. The karyotype (*fig.* 2, C) shows a regular decrease in size, except for the last pair which is strikingly smaller. Four pairs are metacentric (pair 13 being metacentric-submetacentric), 8 are submetacentric (pairs 14 and 17 being submetacentric-meta-

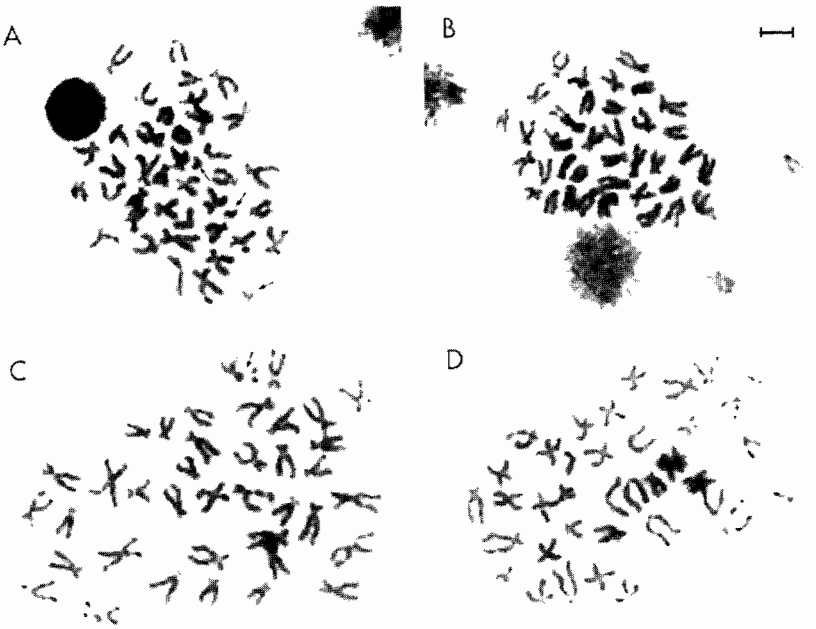

Figure 1. – Mitotic metaphases. A: *Cerastoderma edule*, note three supernumerary chromosomes (arrows); B: *C. edule*, metaphase without supernumerary chromosomes; C: *Venerupis pullastra*, note the secondary constrictions (arrows); D: *Venerupis rhomboides*. Scale bar = 5 µm.

Table 1. – Chromosome measurements and classification derived from ten metaphase cells of *Cerastoderma edule* (m: metacentric; sm: submetacentric; st: subtelocentric; t: telocentric).

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1	7.169	0.454	0.533	0.088	34.418	3.633	sm
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3	6.329	0.356	0.460	0.088	31.150	4.199	sm
4	6.081	0.284	0.404	0.042	28.546	2.134	sm
5	5.849	0.282	0.286	0.037	22.025	2.201	st
6	5.543	0.437	0.457	0.075	30.987	3.689	sm
7	5.489	0.274	0.458	0.100	30.989	4.240	sm
8	5.398	0.307	0.357	0.064	26.090	3.349	sm-st
9	5.273	0.399	0.129	0.040	11.213	3.074	t-st
10	5.073	0.187	0.457	0.051	31.072	2.475	sm
11	4.908	0.258	0.385	0.074	27.469	3.745	sm
12	4.906	0.190	0.244	0.058	19.352	3.789	st
13	4.821	0.235	0.309	0.056	23.355	3.343	st
14	4.711	0.204	0.315	0.046	23.760	2.687	st
15	4.582	0.294	0.353	0.064	25.793	3.519	sm-st
16	4.565	0.233	0.603	0.081	37.199	3.348	sm-m
17	4.474	0.259	0.142	0.045	12.272	3.340	t-st
18	4.205	0.309	0.342	0.061	25.208	3.372	sm-st
19	4.145	0.541	0.162	0.116	12.368	5.424	t-st

homologous chromosomes or on one chromosome only.

Venerupis rhomboides

The chromosomes of 57 mitotic metaphases (*fig.* 1, D) taken from 15 animals were counted. 45 cells had $2n = 38$, the remaining being aneuploid ($2n = 35$-37). Means and SD of RI, Ar and Ci are given in *table* 3. The karyotype (*fig.* 2, C) shows a regular decrease in size, except for the last pair which is strikingly smaller. Four pairs are metacentric (pair 13 being metacentric-submetacentric), 8 are submetacentric (pairs 14 and 17 being submetacentric-meta-

Figure 2. – Karyotypes A: *C. edule*; B: *V. pullastra*; C: *V. rhomboides*. Scale bar = 5 µm.

centric), 4 are subtelocentric (pairs 3 and 19 being subtelocentric-submetacentric) and 3 are telocentric (*fig.* 4). Lightly staining telomeres were sometimes observed on the long arms of the submetacentric pair 16.

DISCUSSION

The diploid number of $2n=38$ recorded in the three veneroid species studied is common among the Superorder Veneroida (Thiriot-Quiévreux *et al.*, 1987). For *C. edule*, previous reports have given $2n=38$ (Koulman and Wolff, 1977) and $2n=40$ (Rasotto *et al.*, 1981). Our data here are the first recorded for *V. pullastra* and *V. rhomboides*.

Karyological data are given in the Cardiidae only in the paper by Koulman and Wolff (1977) who described the chromosomes of *C. edule* (originating from the Delta Area, Netherlands) in two mitotic cells. These authors distinguished 7 submetacentric,

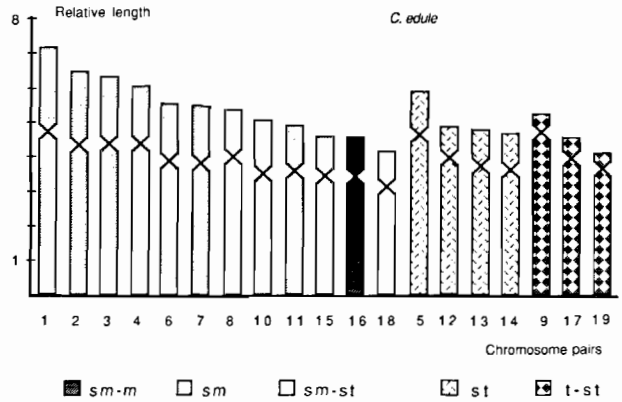

Figure 3. – Ideogram constructed from relative length and centromeric index values in *C. edule*.

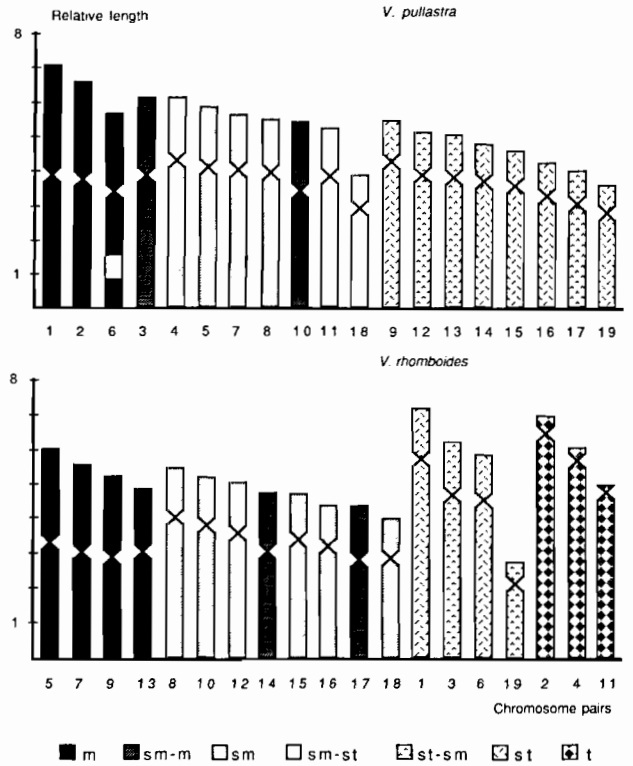

Figure 4. – Ideograms constructed from relative length and centromeric index values in *V. pullastra* and *rhomboides*. *V. pullastra:* pair 10 is submetacentric-metacentric. *V. rhomboides:* pairs 14 and 17 are submetacentric-metacentric.

7 subtelocentric and 5 telocentric chromosome pairs. Our results, based on morphometric measurements of chromosomes, confirm the absence of metacentric chromosomes in this species, but differ in the proportion of submetacentric, subtelocentric and telocentric (12 sm, 4 st, 3 t). Our observations on the occurrence of supernumerary chromosomes (or B-chromosomes) in the Baldayo population of *C. edule* were also recorded in another population, originating from Ria del Pasaje (NW Iberian Peninsula). Out of 153 metaphases scored (taken from 10 animals), 57 cells showed B-chromosomes (Insua and Thiriot-Quiévreux, unpublished data). *C. edule* is the first bivalve species where true supernumerary chromosomes or B-chromosomes were observed. These structures occur particularly often in plants and insects (White, 1973), but they have also been noted in fishes (e.g. Pauls and Berthello, 1990), reptilians (e.g. Kupriyanova, 1980) and mammals (e.g. Volubujev, 1980). They are characterized by intra and inter-individual variations, as well as inter-populational variations (White, 1973). Investigations of B-chromosomes in populations of the common western European cockles *C. edule*, *C. lamarcki* and *C. glaucum* may provide new information regarding the taxonomy and genetics of this

Table 2. – Chromosome measurements and classification derived from ten metaphase cells of *Venerupis pullustra* (m: metacentric; sm: submetacentric; st: subtelocentric; t: telocentric).

Chromosome pair No.	Relative length		Arm ratio		Centromeric index		Classification
	Mean	SD	Mean	SD	Mean	SD	
1	7.073	0.235	0.842	0.058	45.573	1.720	m
2	6.590	0.311	0.770	0.060	43.361	1.913	m
3	6.149	0.348	0.601	0.070	37.333	2.795	sm-m
4	6.131	0.248	0.436	0.044	30.184	2.187	sm
5	5.883	0.266	0.437	0.037	30.289	1.735	sm
6	5.672	0.330	0.669	0.106	39.740	3.692	m
7	5.635	0.214	0.404	0.063	28.533	3.248	sm
8	5.484	0.260	0.399	0.105	28.027	5.159	sm
9	5.444	0.183	0.292	0.074	22.273	4.419	st
10	5.414	0.211	0.603	0.065	37.364	2.440	sm-m
11	5.216	0.185	0.363	0.076	26.323	4.115	sm-st
12	5.118	0.138	0.336	0.074	24.846	4.023	st-sm
13	5.056	0.159	0.335	0.046	24.853	2.466	st-sm
14	4.787	0.145	0.308	0.060	23.302	3.403	st
15	4.577	0.201	0.294	0.036	22.534	2.174	st
16	4.258	0.222	0.306	0.040	23.116	2.287	st
17	4.021	0.196	0.330	0.048	24.694	2.730	st-sm
18	3.903	0.238	0.351	0.063	25.718	3.364	sm-st
19	3.590	0.220	0.298	0.033	22.821	1.981	st

Table 3. – Chromosome measurements and classification derived from ten metaphase cells of *Venerupis rhomboides* (m: metacentric; sm: submetacentric; st: subtelocentric; t: telocentric).

Chromosome pair No.	Relative length		Arm ratio		Centromeric index		Classification
	Mean	SD	Mean	SD	Mean	SD	
1	7.259	0.388	0.270	0.064	20.971	3.887	st
2	7.007	0.484	0.080	0.018	7.307	1.559	t
3	6.207	0.258	0.337	0.065	24.928	3.825	st-sm
4	6.089	0.342	0.069	0.023	6.371	1.953	t
5	6.052	0.276	0.853	0.067	45.842	1.868	m
6	5.879	0.245	0.304	0.044	23.134	2.449	st
7	5.600	0.250	0.854	0.066	45.912	1.967	m
8	5.503	0.433	0.372	0.055	26.945	2.813	sm
9	5.261	0.211	0.826	0.050	45.038	1.463	m
10	5.201	0.230	0.385	0.060	27.600	3.246	sm
11	5.012	0.160	0.052	0.023	4.839	1.996	t
12	4.990	0.288	0.405	0.042	28.658	2.023	sm
13	4.897	0.292	0.630	0.049	38.470	1.935	m-sm
14	4.772	0.357	0.581	0.089	36.495	3.409	sm-m
15	4.704	0.276	0.400	0.053	28.336	2.617	sm
16	4.398	0.362	0.389	0.058	27.734	2.996	sm
17	4.397	0.509	0.580	0.070	36.504	2.776	sm-m
18	4.001	0.225	0.411	0.053	28.789	2.553	sm
19	2.771	0.204	0.311	0.083	23.250	4.701	st-sm

Table 4. – Comparative analysis of karyotypes in five species of Tapetinae (m: metacentric; sm: submetacentric; st: subtelocentric, t: telocentric).

Species	Haploid number	Karyotype				References
		m	sm	st	t	
Ruditapes philippinarum (Adams & Reeve, 1850)	19	9	10			Borsa and Thiriot-Quiévreux, 1990
Venerupis aurea (Gmelin, 1791)	19	8	9	1	1	Borsa and Thiriot-Quiévreux, 1990
Ruditapes decussatus (Linnaeus, 1758)	19	6	3	10		Borsa and Thiriot-Quiévreux, 1990
Venerupis pullastra (Montagu, 1803)	19	3	8	8		Present study
Venerupis rhomboides (Pennant, 1777)	19	4	8	4	3	Present study

species complex, named *Cardium* (*Cerastoderma*) spp. by Brock (1989, 1991).

Among the Veneridae, karyotypes and morphometric measurements of chromosomes have been given for three other species of the same subfamily, the Tapetinae (Borsa and Thiriot-Quiévreux, 1990). A comparative analysis of Tapetinae karyotypes is given *table* 4 (the nomenclature used follows the FAO identification sheets, Fischer *et al.*, 1987). The five species are clearly distinguished by their different proportions of metacentric, submetacentric, subtelocentric and telocentric chromosome pairs. In order to evaluate the relationship between species, a two-step analysis was made: (*i*) a Principal Component Analysis (PCA) on the relative length and centromeric index for the five species studied (data in *tables* 2 and 3, this paper, and in *tables* 2, 3, and 4, Borsa and Thiriot-Quiévreux, 1990). This first step was used to retain the most significant part of the information. (*ii*) a Ward hierarchical classification (Ward, 1963) on the component scores of the species on the axes I and II of the PCA (respectively 43.7% and 28.9% of the variance). This hierarchical grouping "to optimize an objective function" (Ward, 1963) is used to represent distance data in the form of an ultrametric tree (Swofford and Olsen, 1990). These methods were computed with the BIOMECO software (Centre d'Études Physico-sociologiques et Ecologiques, CEPE-CNRS Montpellier). *Figure* 5 gives the dendrogram derived from this hierarchical classification. *V. pullastra* and *R. decussatus* are most closely related, followed by *V. aurea* while *R. philippinarum* and *V. rhomboides* constitute two separate stems with a considerable dissimilarity. These karyological relationships may suggest that *V. aurea*, *R. decussatus* and *V. pullastra* might be more suitable for hybridization experiments than *R. philippinarum* and *V. rhomboides*.

This analysis of morphometric measurements of chromosomes in five species of Tapetinae suggests the

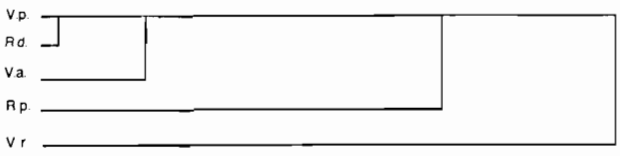

Figure 5. – Dendrogram from a hierarchical analysis of five species of Tapetinae. V.p.: *Venerupis pullastra*, R.d.: *Ruditapes decussatus*; V.a.: *Venerupis aurea*; R.p.: *Ruditapes philippinarum;* V.r.: *Venerupis rhomboides*.

separation into three taxons of the species studied, corresponding to (1) *R. philippinarum*, (2) *V. rhomboides* and (3) the remaining species pooled within a single group. However, the taxonomy of the clam species of Tapetinae, based on morphological characters, varies according to different authors. Three different genera are now used: *Venerupis*, *Tapes* and *Ruditapes*, and the species are named according to one or the other genus (*see* for synonymies Fischer-Piette and Métivier, 1971; Partridge, 1977). According to the taxonomic revision of Tapetinae, made by Fischer-Piette and Métivier (1971), our karyological inferences are in agreement with the separation of *R. philippinarum* and *V. rhomboides* (= *Tapes rhomboides* Pennant, 1777 in their paper) but differ in the case of *R. decussatus*, which is pooled with *V. pullastra* and *V. aurea* in our study but is included in the genus *Ruditapes* with *R. philippinarum* in the work by Fischer-Piette and Métivier, 1971. Therefore, our study provides karyological information which can be used, together with allozyme and morphological data, to investigate the relationships between species within this group.

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