

Chromosomes of Some Subantarctic Brooding Bivalve Species

by

CATHERINE THIRIOT-QUIEVREUX

Université P. et M. Curie, Station Zoologique, 06230 Villefranche-sur-Mer, France

JACQUES SOYER AND MARC BOUVY

Université P. et M. Curie, Laboratoire Arago, UA 117, 66650 Banyuls-sur-Mer, France

AND

JOHN A. ALLEN

University Marine Biological Station Millport, Isle of Cumbrae, Scotland KA28 0EG

Abstract. Chromosomes of three subantarctic brooding bivalve species have been studied in relation to their type of development and the evolutionary distance between their taxonomic categories. *Gaimardia trapesina* (Gaimardiidae) has a diploid chromosome number of $2n = 38$, with 8 chromosome pairs of metacentrics, 7 pairs of submetacentrics, and 4 pairs of subtelocentrics. *Kidderia bisulcata* (Cyamiidae) has $2n = 38$, with 3 pairs of metacentrics, 4 pairs of submetacentrics, 7 pairs of subtelocentrics, and 5 pairs of telocentrics. *Kidderia minuta*, another species of Cyamiidae, has $2n = 36$, with 3 pairs of metacentrics, 2 pairs of submetacentrics, 8 pairs of subtelocentrics, and 5 pairs of telocentrics. The karyological features of these species are not related to direct development and the brooding of the developing eggs. Evolutionary considerations based on comparison of the chromosomes of the families investigated (the Gaimardiidae and the Cyamiidae) suggest that they are phylogenetically primitive. The recent transfer of *Kidderia bisulcata* (= *Hiatella bisulcata*) from the Hiatellidae (Myoida) to the Cyamiidae (Veneroida) is questioned, and further morphological study is required to determine its true taxonomic position. It is also clear that the evolutionary pattern of karyological features remains unsatisfactory without further investigations of eulamellibranch species.

INTRODUCTION

Cytogenetic studies of chromosome number and morphology might not only show genetic variation between species and populations, but also evolutionary relationships within different taxonomic groups. The knowledge of the chromosomes in the Bivalvia has increased over the last 15 years. NAKAMURA (1985) reviewed recent investigations on chromosomes of 125 bivalve species belonging to 22 of the 102 Recent families. Of these 125 species, 73 belong to the Mytilidae, Pectinidae, Ostreidae, and Unionacea; the other species are scattered mostly within the Pteriomorpha, with fewer within the Heterodonta. Thus, evolutionary interpretation of karyological characteristics re-

mains hazardous without further investigations, especially as the chromosomes of the primitive groups of bivalves have rarely been investigated. Exceptions are two species of Solemyidae (IEYAMA, 1982) and seven species of Arcidae (IEYAMA, 1975, 1983, 1984a, b). A further point of interest concerning primitive bivalves is that non-planktotrophic development appears to be the rule for primitive groups, such as the Protobranchia, Septibranchia, and the eulamellibranch superfamilies Lucinacea and Crassatellacea (JABLONSKI & LUTZ, 1983). Most other bivalve species have planktotrophic development.

Non-planktotrophic development combined with brood protection constitutes a specialized type of development that occurs among some primitive superfamilies (Arcacea,

Leptonacea, and Cyamiacea). Antarctic Bivalvia have a relatively large percentage of species within these superfamilies (DELL, 1972; ARNAUD, 1974; RICHARDSON, 1979).

In a research program on the evolutionary genetics of benthic species from the subantarctic Kerguelen Islands, we selected four species (with direct development and brooding of young) in order to study their chromosomes and to appreciate whether their karyological features may reflect a development type or a phylogenetic trend.

The present paper gives karyological data on three of these species, namely: *Gaimardia trapesina* (Lamarck, 1819) (Heterodonta, Veneroida, Gaimardiacea, Gaimardiidae); *Kidderia bisulcata* (Smith, 1879); and *Kidderia minuta* (Dall, 1876) (Heterodonta, Veneroida, Cyamiacea, Cyamiidae). Because of their peculiar characteristics, the chromosomes of the fourth species investigated, *Lasaea consanguinea* (Smith, 1877) (Heterodonta, Veneroida, Leptonacea, Lasaeidae), are to be described in a separate paper.

Classification follows NEWELL, 1969 (see also, OLDFIELD, 1964; PONDER, 1967; SIMPSON, 1977; MORTON, 1979; RICHARDSON, 1979; BOSS, 1982; O'FOIGHIL, 1986). Detailed comparisons have been made with Antarctic material housed in the British Museum (Natural History).

MATERIALS AND METHODS

Sampling

Populations of *Kidderia minuta* were collected by hand at low tide in the intertidal zone under rocks in a well sheltered area "Halage des Swains," in the southwest part of the Gulf of Morbihan, Kerguelen Islands.

Specimens of *Kidderia bisulcata* and *Gaimardia trapesina* were collected among algae in minute pools of a small reef, exposed only at low tide at Ratmanoff, on the east coast of the Kerguelen Islands.

Chromosome Preparations

Whole animals were treated 2–4 h with 0.005% colchicine in seawater. Then the bodies were removed from their shells under the dissecting microscope and treated 40 min in 0.9% sodium citrate. The material was then fixed in a freshly prepared mixture of absolute alcohol and acetic acid (3:1) with three changes of 20 min duration. Each slide preparation was made from three to five bodies following an air-drying technique (THIRIOT-QUIÉVREUX & AYRAUD, 1982). The preparations were stained with Giemsa (4%, pH 6.8) and photographs of suitable metaphases were taken with a Zeiss II photomicroscope. Cell divisions were mainly observed in gonadic tissue.

Data Analysis

The number of chromosomes seen in the photomicrographs of at least 30 spread metaphases were counted for each species. Then the photographs of individual chro-

mosomes from the better spreads were cut out and arranged in pairs on the basis of size and centromere position for the karyotypes.

Measurements of chromosomes were made with a digitizer (Bit Pad 10, Summa graphic), interfaced with a Victor S1 microcomputer (THIRIOT-QUIÉVREUX, 1984). Relative length or percent total complement length was expressed as 100 times the absolute chromosome pair length divided by the total length of the haploid complement. Centromeric indexes (C_i) were calculated by dividing 100 times the length of the short arm by the total chromosome length. Terminology relating to centromeric position follows that of Levan *et al.* (1964). A chromosome is metacentric (m) if C_i falls in the range 37.5–50.0, submetacentric (sm) if C_i is 25.0–37.5, subtelocentric (st) if C_i is 12.5–25.0, and telocentric (t) if C_i is 0.0–12.5. When a centromere position was found to be on the borderline between two different categories the confidence limit of the means was calculated as $P = 0.05$ and two chromosome categories are listed. The arm ratio is calculated as length of short arm divided by the length of the long arm. The centromeric index and the arm ratio are given, as both express centromeric position and allow comparison with previous studies.

RESULTS

Gaimardia trapesina

The chromosomes of 31 mitotic metaphase spreads were counted. Seventeen cells showed $2n = 38$, 14 cells had an aneuploid number of 33 to 37. A haploid number of 19 was counted in three meiotic metaphases. Thus the diploid chromosome number for this species is $2n = 38$.

Means and standard deviations of relative length, arm ratio, and centromeric index for seven well-spread metaphases from different animals are given in Table 1.

From data on relative length, we recognize five groups of chromosome pairs of decreasing size and, from the centromeric index, we characterize the morphological type of each chromosome pair. Thus, the karyotype (Figure 1) of *Gaimardia trapesina* consists of:

- Group I: pair 1 metacentric, obviously larger than the remainder.
- Group II: pairs 2, 3, 4, 5, 7 submetacentric; pair 6 subtelocentric.
- Group III: pairs 8 and 9 submetacentric; pair 10 subtelocentric to submetacentric, pair 11 subtelocentric.
- Group IV: pairs 12 to 15 metacentric.
- Group V: pairs 16 to 18 metacentric and pair 19 subtelocentric.

In order to visualize better the different types of chromosome pairs, we have constructed an ideogram from centromeric indexes and relative length values. The ideogram for *Gaimardia trapesina* (Figure 2) shows a conspicuous

Table 1
Chromosome measurements and classification in seven cells for *Gaimardia trapesina*.

Group	Chromosome pair number	Relative length		Arm ratio		Centromeric index		Classification
		Mean	SD	Mean	SD	Mean	SD	
I	1	11.92	0.914	0.811	0.058	44.61	1.858	m
II	2	6.69	0.307	0.464	0.043	31.53	1.979	sm
II	3	6.23	0.308	0.413	0.054	29.00	2.800	sm
II	4	6.11	0.258	0.448	0.043	30.66	2.153	sm
II	5	5.87	0.269	0.490	0.051	32.73	2.379	sm
II	6	5.61	0.523	0.306	0.059	23.19	3.567	st
II	7	5.51	0.494	0.428	0.120	28.43	4.166	sm
III	8	5.21	0.438	0.506	0.050	33.34	2.264	sm
III	9	5.11	0.501	0.478	0.051	32.11	2.357	sm
III	10	5.06	0.614	0.335	0.088	24.70	4.834	st-sm
III	11	4.75	0.726	0.296	0.061	22.57	3.577	st
IV	12	4.49	0.433	0.810	0.115	44.38	3.569	m
IV	13	4.33	0.279	0.873	0.077	46.23	2.131	m
IV	14	4.19	0.383	0.848	0.150	45.40	4.219	m
IV	15	4.11	0.541	0.819	0.173	44.28	6.271	m
V	16	3.91	0.304	0.937	0.698	48.08	1.794	m
V	17	3.80	0.223	0.893	0.158	46.44	4.536	m
V	18	3.66	0.318	0.861	0.061	45.90	1.745	m
V	19	3.37	0.456	0.295	0.110	22.14	6.862	st

disparity of size between the pair 1 and the other pairs. Three different types of chromosomes are present: metacentric, submetacentric, and subtelocentric.

We summarize karyological data for this species with the formula: $2n = 38 = 8m, 7sm, 4st = 15m-sm/4st$.

Kidderia bisulcata

The chromosome of 35 mitotic metaphases were counted. Twenty-eight cells had $2n = 38$, 7 cells had $2n = 36$ or 37. Meiotic metaphases were abundant and we scored 36 cells, of which 32 showed a haploid number of 19 and

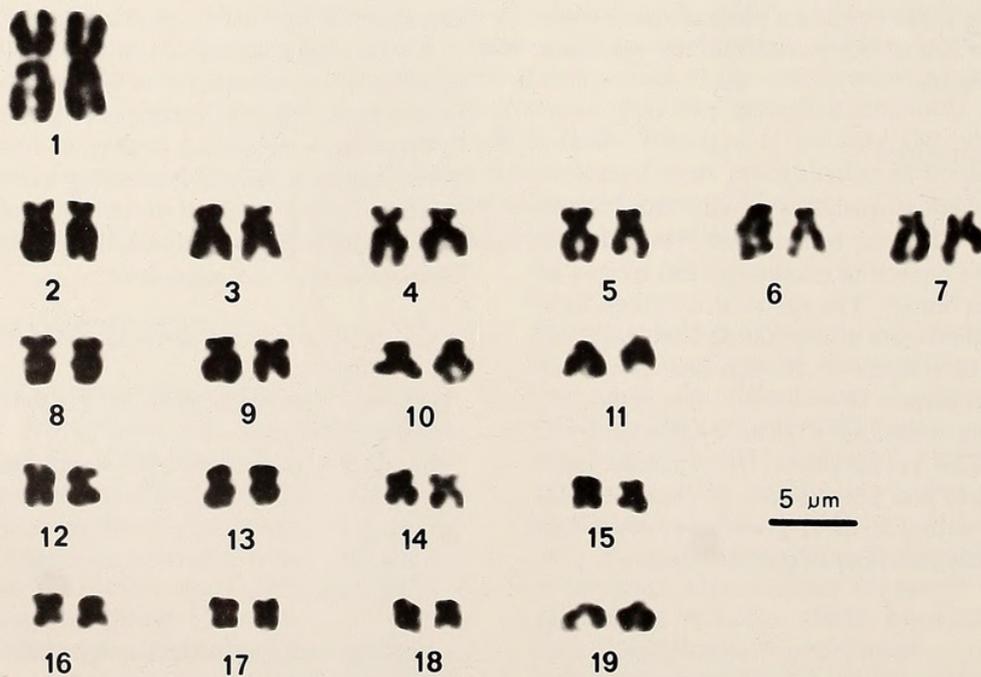


Figure 1

Karyotype of *Gaimardia trapesina*.

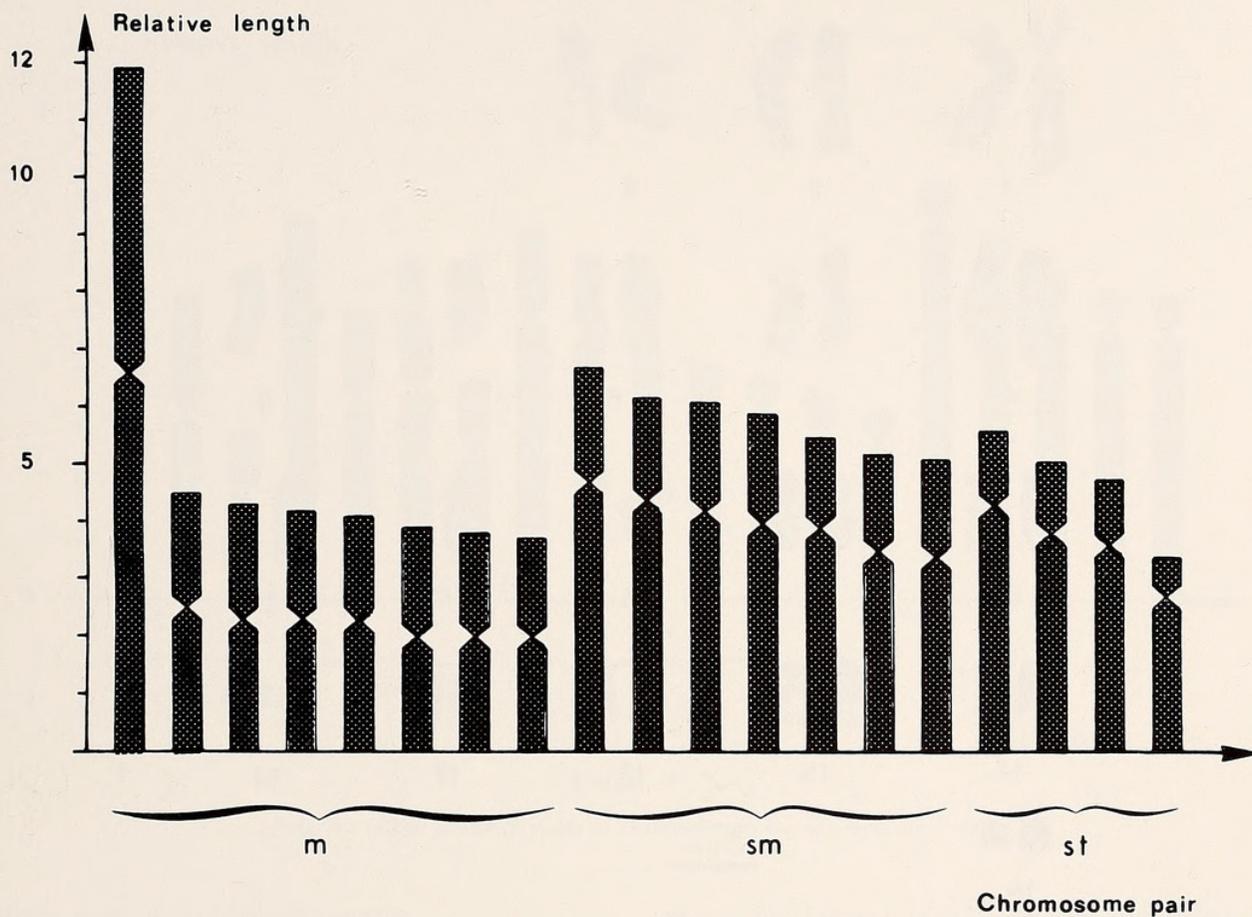


Figure 2

Ideogram of the different types of chromosomes for *Gaimardia trapalina*.

Table 2

Chromosome measurements and classification in eight cells for *Kidderia bisulcata*.

Group	Chromosome pair number	Relative length		Arm ratio		Centromeric index		Classification
		Mean	SD	Mean	SD	Mean	SD	
I	1	8.24	1.075	0.685	0.180	39.76	6.603	m
I	2	7.27	0.535	0.102	0.015	9.24	1.294	t
I	3	6.65	0.272	0.425	0.163	28.49	6.714	sm
II	4	6.39	0.522	0.107	0.034	9.55	2.783	t
II	5	6.38	0.437	0.309	0.107	23.01	5.987	st
II	6	6.05	0.370	0.288	0.118	21.78	6.193	st
II	7	5.69	0.534	0.129	0.028	11.40	2.216	t-st
II	8	5.66	0.282	0.213	0.172	15.71	6.901	st
III	9	5.36	0.155	0.127	0.027	11.15	2.114	t-st
III	10	5.33	0.469	0.139	0.028	12.11	2.138	t-st
III	11	5.32	0.356	0.695	0.105	39.68	5.743	m
III	12	4.99	0.343	0.435	0.076	29.76	3.106	sm
III	13	4.95	0.323	0.343	0.081	25.03	4.591	sm-st
IV	14	4.13	0.593	0.180	0.041	15.09	2.968	st
IV	15	3.91	0.350	0.199	0.083	16.01	4.778	st
IV	16	3.85	0.449	0.455	0.092	30.80	4.600	sm
IV	17	3.54	0.564	0.196	0.055	16.10	3.773	st
IV	18	3.35	0.470	0.203	0.045	16.56	2.944	st
V	19	2.86	0.324	0.709	0.180	40.51	6.382	m

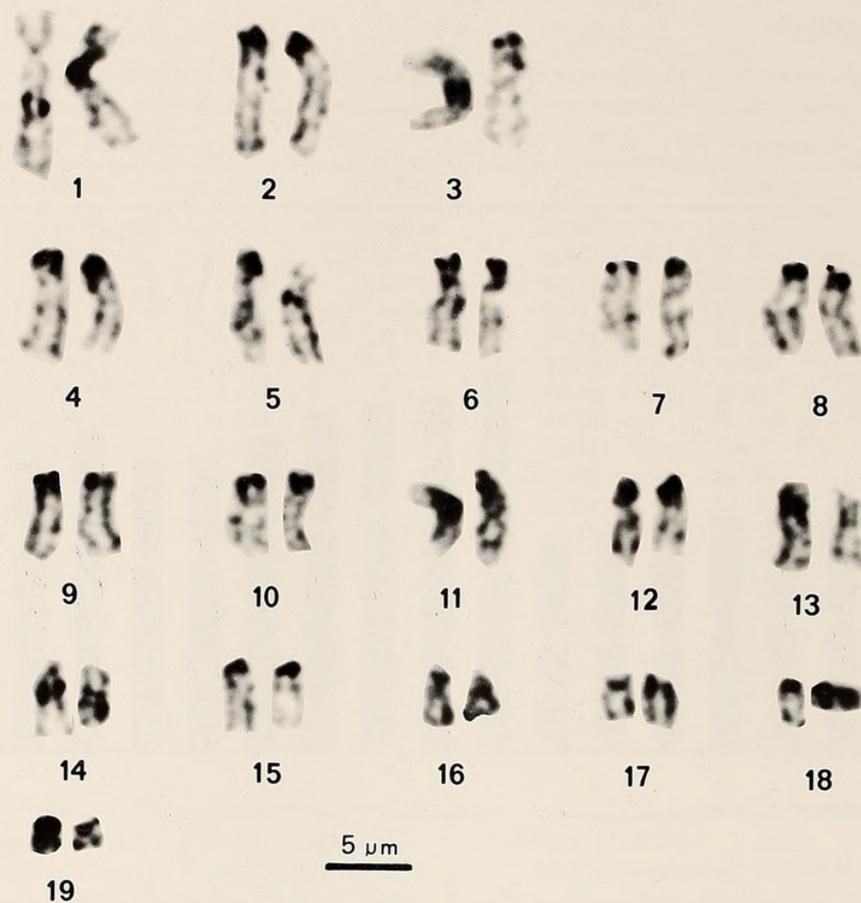


Figure 3

Karyotype of *Kidderia bisulcata*.

2 with 18. Thus, the diploid chromosome number for this species is $2n = 38$.

For karyotyping, eight well-spread metaphases from different animals were analyzed (Table 2). The karyotype (Figure 3) of *Kidderia bisulcata* consists of five groups of chromosome pairs with a regular decrease in size:

Group I: pair 1 metacentric, pair 2 telocentric, pair 3 submetacentric.

Group II: pairs 4–8 submetacentric or telocentric. The pairs 4 and 5, 7 and 8 are very close in relative length and it is difficult to identify them with rigor; however, the position of the centromere is always telocentric in pair 4 and telocentric to submetacentric in pair 7.

Group III: pairs 9 and 10 are very similar, telocentric to submetacentric, pair 11 metacentric, pair 12 submetacentric, pair 13 submetacentric–subtelocentric. The last two pairs are also very similar and can be confused.

Group IV: pairs 14 and 15 submetacentric, pair 16 submetacentric, pairs 17 and 18 subtelocentric.

Group V: pair 19 metacentric and obviously the smallest.

The ideogram (Figure 4) shows the distribution of the four chromosome types. We summarize karyological data

for this species with the formula: $2n = 38 = 3m, 4sm, 7st, 5t = 7m-sm/12st-t$.

Kidderia minuta

The chromosomes of 36 mitotic metaphases were counted. Twenty-nine cells had $2n = 36$, 7 cells had an aneuploid diploid number varying from 32 to 36. Ten meiotic metaphases were also counted, 9 with $n = 18$, 1 with $n = 19$. The diploid chromosome number for this species is $2n = 36$.

The chromosome measurements and classification were analyzed for seven examples of well-spread metaphases, each from a different animal (Table 3).

The karyotype (Figure 5) consists of six groups of chromosome pairs of decreasing size, the first group being much larger than the other groups, for the latter rank order of decreasing size is relatively regular:

Group I: pair 1 metacentric.

Group II: pair 2 telocentric, pair 3 metacentric, pairs 4 and 5 telocentric.

Group III: pair 6 submetacentric–subtelocentric, pair 7 telocentric, pair 8 metacentric, pair 9 telocentric.

Group IV: pairs 10 to 12 subtelocentric.

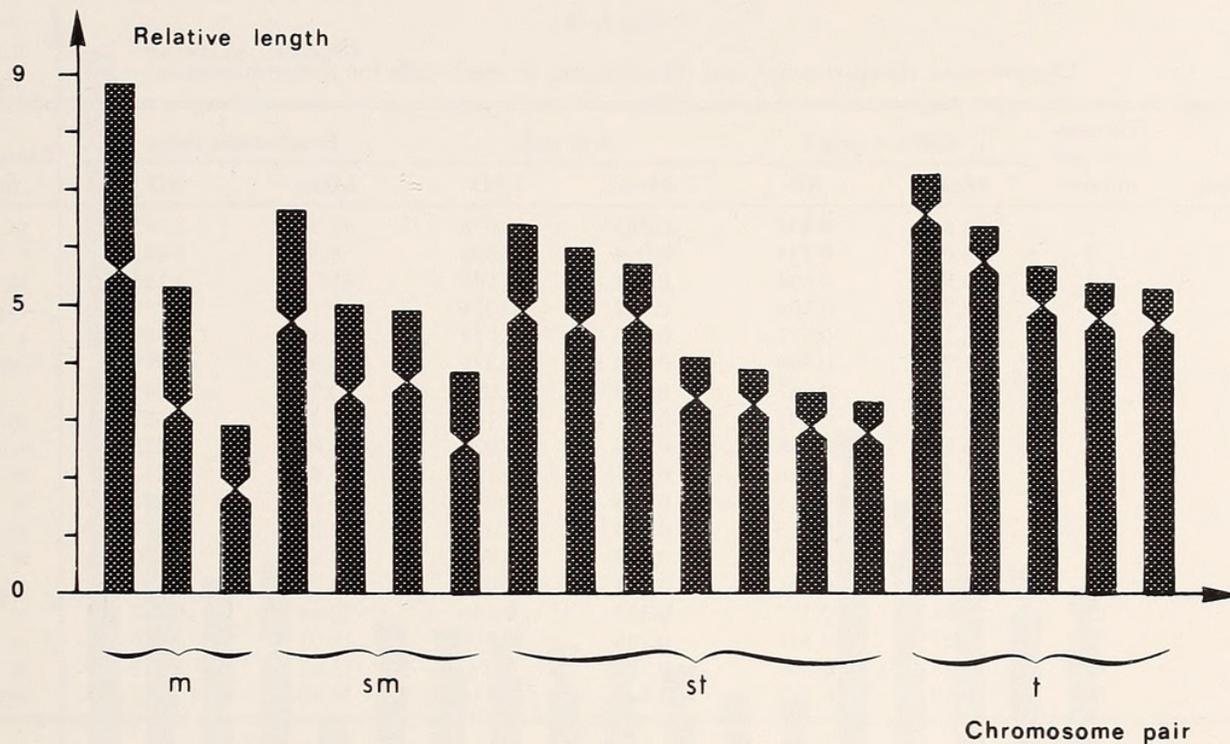


Figure 4

Ideogram of the different types of chromosomes for *Kidderia bisulcata*.

Group V: pairs 13 to 15 subtelocentric.

Group VI: pairs 16 and 17 subtelocentric, pair 18 submetacentric-metacentric.

The ideogram (Figure 6) clearly shows the disparity of size between pair 1 and the other pairs. Four morphological types of chromosomes are present but subtelocentric and telocentric types are dominant in this species.

We summarize karyological data for this species with the formula: $2n = 36 = 3m, 2sm, 8st, 5t = 5m-sm/13st-t$.

DISCUSSION

There is considerable debate in the literature as to the exact relationships of the Gaimardiacea and the Cyamiacea (MORTON, 1979). Until recently, both superfamilies were included in the Veneroidea although widely separated in the classification of the order (NEWELL, 1969). MORTON (1979) in his study on *Neogaimardia finlayi* questioned this and concluded that the gaimardiids were closely related to the cyamiids, however, admitting that more comprehensive studies were necessary to be certain. PONDER (1971) included the Gaimardiinae as a subfamily in the Cyamiacea. Furthermore, BOSS (1982) transferred the genus *Kidderia* from the subfamily Gaimardiinae to the family Cyamiidae and, following PONDER (1971), he reinstated the Gaimardiidae to family rank.

The problem is further complicated by the fact that *Kidderia bisulcata* was originally described as a species of *Saxicava* (= *Hiattella*) by SMITH (1879). It was still regarded

as such by POWELL (1957) but later considered to be a species of *Kidderia* by DELL (1969). The shell features, including radial grooves, elongate opisthodontic ligament, and hinge structure, would lead one to conclude that it is a hiattellacean species. In contrast, *K. minuta* has no radial grooves and a much thinner hinge plate with cardinal teeth of a different form, although the opisthodontic ligament (more internal in position) is massive and elongate.

Although detailed morphological comparisons need to be carried out, comparison of the karyological data of these three brooding bivalve species does not show close relationship. Moreover, a fourth brooding species investigated, *Lasaea consanguinea*, is totally different, in showing an unusually high number of chromosomes (THIRIOT-QUIÉVREUX *et al.*, in press).

Karyological features are generally species specific and consequently could be related to the evolutionary distance between taxonomic categories. Chromosome data for veneroid bivalves are only recorded for more recent families, such as the Cardiidae, Mactridae, Donacidae, Corbiculidae, Pisididae, and Veneridae (NAKAMURA, 1985) and the diploid chromosome complement is $2n = 36$ or $2n = 38$ (except for the Pisididae). Three species of Veneridae have been karyologically investigated and show $2n = 38 = 19m-sm$ (IEYAMA, 1980). We have found the same karyological data for *Ruditapes philippinarum*, another venerid species (personal observations). Nevertheless, within the Cardiidae, a family with a more primitive phylogenetic position, one species, *Cerastoderma edule*, shows karyological data

Table 3
Chromosome measurements and classification in seven cells for *Kidderia minuta*.

Group	Chromosome pair number	Relative length		Arm ratio		Centromeric index		Classification
		Mean	SD	Mean	SD	Mean	SD	
I	1	14.64	0.836	0.783	0.070	43.55	2.393	m
II	2	8.04	0.734	0.094	0.022	8.57	1.842	t
II	3	6.87	0.697	0.851	0.108	45.73	3.134	m
II	4	6.75	0.709	0.102	0.024	9.18	2.059	t
II	5	6.17	0.577	0.106	0.014	9.57	1.168	t
III	6	5.75	0.599	0.374	0.075	26.89	3.999	sm-st
III	7	5.61	0.367	0.123	0.019	10.91	1.541	t
III	8	5.38	0.591	0.751	0.148	42.31	4.657	m
III	9	5.24	0.348	0.124	0.028	10.89	2.215	t
IV	10	4.68	0.366	0.311	0.122	21.84	5.232	st
IV	11	4.57	0.211	0.155	0.045	13.31	3.176	st
IV	12	4.49	0.245	0.154	0.022	13.23	1.627	st
V	13	4.24	0.227	0.173	0.043	14.60	3.160	st
V	14	3.98	0.201	0.153	0.022	13.23	1.732	st
V	15	3.86	0.332	0.327	0.130	22.68	5.947	st
VI	16	3.39	0.441	0.166	0.046	14.01	3.476	st
VI	17	3.28	0.308	0.186	0.050	15.41	3.542	st
VI	18	2.99	0.415	0.643	0.336	36.40	14.695	sm-m

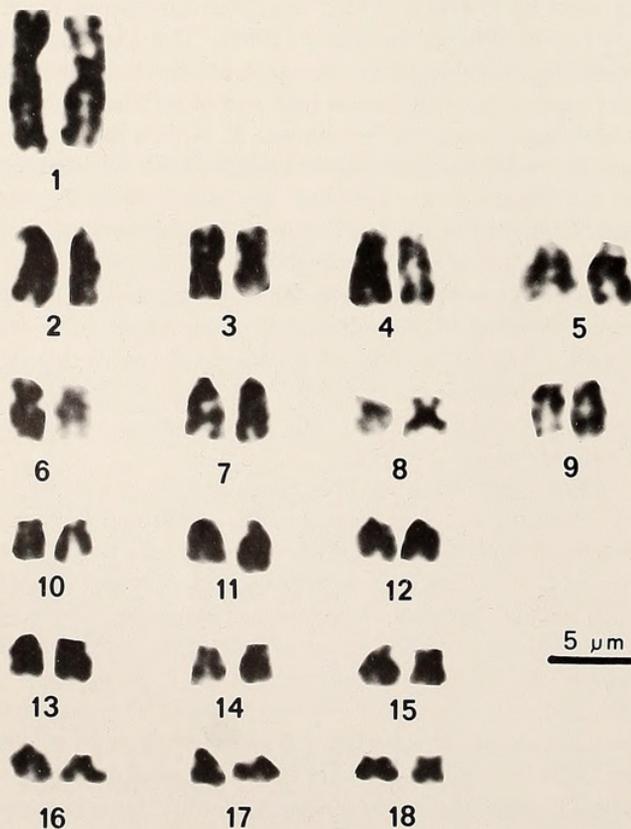


Figure 5

Karyotype of *Kidderia minuta*.

of $2n = 38 = 7sm/12st-t$ (KOULMAN & WOLFF, 1977). The two species of the family Cyamiidae studied here, *Kidderia bisulcata* with $2n = 38 = 7m-sm/12st-t$ and *K. minuta* with $2n = 36 = 5m-sm/13st-t$ are karyologically closer to the Cardiidae than to the Veneridae so far investigated. As reported above there is some doubt as to whether *K. bisulcata* is a cyamiid, but both species are characterized by a variable diploid complement and the presence of the four chromosomal types, the majority being st-t.

A variable number of chromosomes combined with the presence of st-t chromosomes reflects variable karyotypes (WHITE, 1973). In contrast, a majority of m-sm chromosomes suggests a stable karyotype (NAKAMURA, 1985). Thus, the karyotypes of two species of Cyamiidae and one species of Cardiidae seem less stable than those of karyologically known species of the family Veneridae. *Gaimardia trapesina*, with a majority of metacentrics, submetacentrics, and a few subtelocentrics, could tentatively be considered to show a more stable karyotype and therefore have an intermediate position between the Cyamiidae and the Veneridae. But without further investigation of other species of the Veneroidea, the evolutionary pattern of karyological features remains incomplete and unsatisfactory.

All the evidence points to the fact that the three species studied here are phylogenetically separated and supports the earlier determinations that the Cyamiacea and Gaimardiacea are distinct from each other. So-called *Kidderia bisulcata* may indeed be a species of *Hiatella* (= *Saxicava*). The issue is made more complex by convergence of form

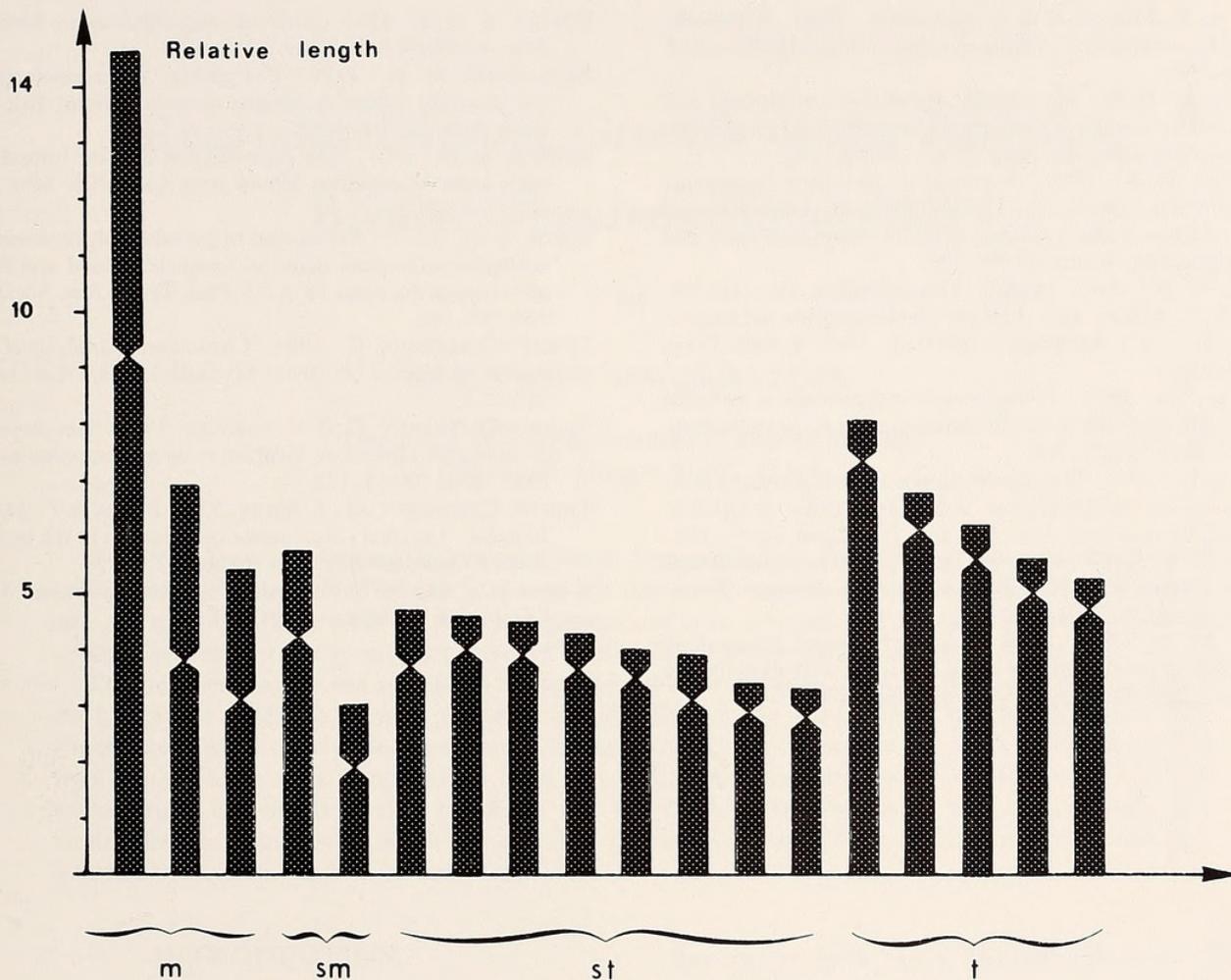


Figure 6

Ideogram of the different types of chromosomes for *Kidderia minuta*.

and reproduction in bivalves of southern high latitudes, which will be the object of further studies.

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