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THE GENUS *HETEROCYPRIS* (CRUSTACEA, OSTRACODA) IN THE
WEST INDIES
PART II. CARAPACE LENGTH, ECOLOGY AND ZOOGEOGRAPHY

by

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SUMMARY

Populations of three species of the genus *Heterocypris*: *H. margaritae* Margalef, 1961, *H. antillensis* Broodbakker, 1982, and *H. punctata* Keyser, 1975, sampled in the Caribbean region are studied. (1) An attempt is made to correlate differences in mean carapace length between samples from different islands and within intra-insular samples, with environmental factors. (2) Differences in the ecology of the three species are determined. (3) The distribution of the three species is discussed. (4) Related species are compared.

Differences in carapace length appear not to be related with genetic differences, but to be caused by environmental influences. In *H. margaritae* correlation was found between carapace length and size (as area) of habitat, and in *H. antillensis* between carapace length and vegetation. Variation in carapace length is probably related with food abundance, pollution and some factors of water chemistry.

H. margaritae is a euryhaline species, living in more permanent habitats of medium size, and in subterranean habitats as well. *H. antillensis* is a freshwater and oligohaline species, living in more temporary, somewhat polluted, open habitats, with a muddy bottom in limestone areas. *H. punctata* is a mesohaline species, dwelling in larger uncovered waterbodies on limestone, with a mud or sandy mud bottom.

H. margaritae has its closest relatives in South America, while *H. antillensis* and *H. punctata* seem to have their closest relatives in the southern part of North America.

RÉSUMÉ

Des populations de trois espèces du genre *Heterocypris* ont été étudiées: *H. margaritae* Margalef, 1961, *H. antillensis* Broodbakker, 1982, et *H. punctata* Keyser, 1975, échantillonnées dans la région des Caraïbes. (1) Les différences remarquées dans la longueur moyenne de la carapace

entre échantillons en provenance soit d'îles diverses, soit de la même île, sont mises en corrélation avec des facteurs du milieu. (2) Les différences dans l'écologie des trois espèces sont déterminées. (3) On discute la distribution géographique des trois espèces. (4) Les espèces apparentées sont comparées.

Les différences dans la longueur de la carapace se montrent non-corrélatives avec des différences génétiques, mais bien avec certains facteurs du milieu. Pour *H. margaritae* une corrélation a été trouvée entre la longueur de la carapace et les dimensions de l'habitat, et pour *H. antillensis* entre la longueur de la carapace et la végétation. Les variations dans la longueur de la carapace sont probablement en relation avec l'abondance de la nourriture, la pollution et certains facteurs hydrochimiques.

H. margaritae est une espèce euryhaline qui habite des milieux plus permanents de dimensions moyennes, y compris des habitats souterrains. *H. antillensis* est une espèce d'eau douce et oligohaline, peuplant des habitats plutôt temporaires, ouverts, avec fond limoneux sur substrat calcaire, et jusqu'à un certain point pollués. *H. punctata* est une espèce mésohaline que l'on trouve dans des pièces d'eau de dimensions plus importantes, ouvertes, avec un fond sablonneux ou limoneux sur substrat calcaire.

H. margaritae a ses proches parents en Amérique du Sud, tandis que les espèces les plus proches de *H. antillensis* et de *H. punctata* semblent peupler les parties méridionales de l'Amérique du Nord.

1. INTRODUCTION

The present article forms the second part of a study on the genus *Heterocypris*. The first part (Broodbakker, 1982) dealt with the taxonomic aspects of the three species of this genus, encountered in samples taken in the Caribbean

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islands. The present part deals with differences in carapace length between different samples, ecology and zoogeography of the three species: *H. margaritae* Margalef, 1961, *H. antillensis* Broodbakker, 1982, and *H. punctata* Keyser, 1975.

Differences between populations in wells, pools and other habitats, and between different islands are examined by comparing mean carapace length of the *Heterocypris* samples. Carapace length has been chosen because there seemed to be considerable difference in size of animals among part of the samples, while other morphological characters appear to be relatively constant.

Mean carapace length is also compared with environmental factors, viz.: depth, area of habitat, chlorinity, soil, bottom, vegetation, water colour, permanency, and light conditions.

Ecological spectra are determined by calculating frequency distributions of the species in the different types or classes of the environmental factors, and comparing these frequency distributions with expected frequencies, by way of a chi-square test.

The three species will be compared with other *Heterocypris* species, especially from North, Central and South America, in an attempt to determine their origin.

The meaning of the presence of the *Heterocypris* species in wells, and competitive relations with other ostracods, will be discussed in a forthcoming paper.

2. MATERIAL AND METHODS

Part of the material used was sampled by Prof. Dr. J. H. Stock and others (including the author), in the period 1973-1982, during various Amsterdam Expeditions to the West Indies. Most of these samples were from wells and other subterranean habitats. Furthermore, about 600 samples collected by Dr. P. Wagenaar Hummelinck in the period 1930-1973, mostly from epigeal habitats, were at our disposal. Later we received some 50 samples from exclusively subterranean habitats in Cuba, collected by Dr. L. Botosaneanu and others in 1969 and 1973, but these samples did not contain specimens of *Heterocypris*.

In the sequel the samples of Stock and Wagenaar Hummelinck are abbreviated as S and WH, respectively. Other

information concerning these samples is provided in part I of this study (Broodbakker, 1982).

From each station yielding more than 10 specimens of *Heterocypris*, a number of full-grown males and females was measured. Measuring was done with a ruler on a sheet of white paper, on which the animals were projected by way of a camera lucida and a Reichert Diapan microscope.

Computer-sorted data on habitat, chlorinity, soil and other environmental information were statistically tested for regression and single classification analysis of variance with the CDC computer of SARA (Stichting Academisch Rekencentrum Amsterdam). Chi-square tests were performed by hand and with a pocket calculator and *t* tests with a programmable pocket calculator.

The chi-square test. — Expected frequencies (F_e) were calculated by multiplying the number of samples containing ostracods, in each type or class (n_i) with the total number of *Heterocypris* samples (n_1), divided by the total number of samples containing ostracods (n_2). So:

$$F_e = \frac{n_i \cdot n_1}{n_2} \text{ (table V).}$$

Sometimes it was necessary to unite types or classes, to get an expected frequency large enough for a chi-square test to be performed. The types and classes used in tables V-VII are the same as those used for calculating correlations in the chapter about size differences.

3. SIZE DIFFERENCES

3.1. General aspects

Examination of the material made it clear that there are large differences in size, measured as carapace length, of full-grown animals, between samples of different islands and between intransular samples. Comparison of mean length using Student's *t* test resulted in highly significant differences between part of the samples. The question is whether these size differences are determined by genetic factors, through microevolution of in some way isolated, small populations, for instance in wells, or whether they are determined by ecological factors, different for each generation and resulting in size differences over the years, even at the same station.

3.2. *Heterocypris margaritae* (table I).

On the island Margarita there are no large differences in carapace length between a covered

well (S 78/332) and a lagoon (WH 18). The specimens collected by Margalef (1961) in pools somewhere along the road from Porlamar to Punta de Piedras, fit in the same size class. Only in S 78/335, an open well, the females are much larger, but here only seven females were caught. On the nearby island group of Los Testigos the animals are larger, compared with most samples from Margarita. Student's t test for WH 18 and WH 30: $t(\sigma\sigma) = 4.93$, $t(\varphi\varphi) = 6.05$, both $p < 0.001$. Only the small sample S 78/335 from Margarita has about the same carapace length as the Los Testigos animals.

On La Blanquilla which is likewise close to Margarita, the species is much larger. On this island there is a relatively large difference in size between populations of two open wells (S 82/07 and S 82/08a), which are situated near each other ($t(\sigma\sigma) = 4.88$, $t(\varphi\varphi) = 11.5$, both $p < 0.001$). But the differences in carapace length between samples from Margarita and from La Blanquilla are even larger in most cases. The difference between the smallest sized sample from La Blanquilla and the sample from Los Testigos is as large as between the samples from La Blanquilla ($t(\sigma\sigma) = 4.88$, $t(\varphi\varphi) = 7.09$, $p < 0.001$).

On Klein Bonaire the specimens found in a sink hole, with subterranean water (WH 61d), are as large as those in a brackish pool sampled in the years 1930 (WH 63b) and 1949 (WH 63d). The specimens from the pool sampled later in 1930 (WH 63x) and in 1955 (WH 63e) are smaller and larger, respectively. Student's t for WH 63b and WH 63x: $t(\sigma\sigma) = 2.41$ ($p < 0.02$), $t(\varphi\varphi) = 3.98$ ($p < 0.001$); for WH 63b and WH 63e: $t(\sigma\sigma) = 3.43$ ($p < 0.01$), $t(\varphi\varphi) = 9.13$ ($p < 0.001$). In this case there is certainly no correlation between size and chlorinity (table I).

Bonaire presents the greatest variation in carapace lengths. Very small specimens occur in the pool WH 898, in the most northern part of the island (fig. 1). This could be a more or less isolated population, because the other stations with *H. margaritae* are all situated in the eastern part of the island (fig. 1, cf. table I).

The shallow open well S 75/14 in the western part of Bonaire is probably the same as station WH 886, or very close to it. Still the differences in carapace length between these samples are rather large. The specimens of the other localities situated close to these stations have mean lengths comparable either with those of S 75/14 or with those of WH 886. Here we find differences in size which can not be genetically determined if this is one population. It seems that the size differences in this case are determined by environmental factors.

In the pool WH 53, near the western coast of Bonaire, the specimens gathered in 1968 are larger than those collected in 1955. In 1967 this pool dried out, while *Cypris decaryi* Gauthier, 1933, was predominant in 1963. WH 54, a pool near WH 53, dried out in 1955. Before that time it was populated by various other species, while in 1963 *H. margaritae* was found together with specimens of *Stenocypris major* (Baird, 1859), *Cypris decaryi*, and one specimen of *H. antillensis*. It could be that the pools have been repopulated with *H. margaritae* from other pools, but it is more probable that the eggs of the species which are presumably very resistant like all Cypridinae eggs (e.g. Sars, 1889; McKenzie, 1971), have survived the dry period and initiated a new population in better times. In that case the size differences can not be determined genetically.

It is possible that there is a small-sized population in the north and a medium- to large-sized population in the south of the island. However, the small size of the animals in the north could possibly be explained by environmental differences as well, instead of genetical differences. The specimens of Klein Bonaire are small- to medium-sized, the length range fits within the limits found in Bonaire. The mean lengths of the carapaces from Bonaire and Klein Bonaire are not correlated with chlorinity.

On Aruba one small-sized population is encountered in WH 104Bc, a slowly overflowing pool. In the water flow leading to this pool (WH 104Ab), the animals are larger. In this case genetic isolation is impossible, so ecological dif-

TABLE I

Mean carapace length, sex ratio, and some environmental data of the different samples containing *Heterocypris margaritae*. Sex ratio is defined as number of males per 100 females.

Station no.	Island or region	Type of habitat	Chlorinity (g Cl ⁻ /l)	Permanency	Date	N of specimens	Sex ratio	Carapace length	
								♂♂ mean ± S.D. (n)	♀♀ mean ± S.D. (n)
S 78/326	Paraguana	covered well	1.6	-	26-V-1978	29	41	0.82 ± 0.02 (5)	0.93 ± 0.02 (13)
S 78/332	Margarita	covered well	3.2	perm.	31-V-1978	54	37	0.81 ± 0.02 (10)	0.91 ± 0.03 (27)
S 78/335	Margarita	open well	0.4	perm.	1-VI-1978	14	71	0.85 ± 0.02 (5)	0.98 ± 0.01 (7)
WH 18	Margarita	lagoon	0.2	semiperm.	16-V-1936	44	86	0.82 ± 0.02 (17)	0.91 ± 0.03 (21)
Margalef	Margarita	pools	-	-	21-IX-1960	-	-	0.79 - 0.85	0.94
WH 30	Los Testigos	pool	0.5	temp.	14-VI-1936	88	70	0.86 ± 0.03 (32)	0.97 ± 0.04 (41)
S 82/07	La Blanquilla	open well	2.7	perm.	19-II-1982	215	38	0.90 ± 0.03 (23)	1.02 ± 0.02 (37)
S 82/08a	La Blanquilla	open well	3.5	perm.	19-II-1982	600	71	0.94 ± 0.03 (32)	1.09 ± 0.03 (32)
S 82/13	La Blanquilla	open well	1.0	perm.	20-II-1982	97	56	0.94 ± 0.02 (36)	1.09 ± 0.02 (36)
WH 61d	Klein Bonaire	cavern water, sink hole	0.4	perm.	3-XII-1963	395	61	0.80 ± 0.02 (19)	0.90 ± 0.03 (20)
WH 63d	Klein Bonaire	pool	12.4	semiperm.	7-IX-1949	78	27	0.81 ± 0.03 (6)	0.93 ± 0.03 (24)
WH 63e	Klein Bonaire	pool	2.6	semiperm.	20-VIII-1955	250	34	0.84 ± 0.04 (15)	1.01 ± 0.05 (23)
WH 63b	Klein Bonaire	material Klie 3, pool	0.7	semiperm.	9-VI-1930	350	62	0.80 ± 0.03 (21)	0.90 ± 0.04 (33)
WH 63x	Klein Bonaire	material Klie 6, pool	-	semiperm.	17-X-1930	500	21	0.77 ± 0.05 (25)	0.86 ± 0.03 (36)
WH 898	Bonaire	pool	3.0	semiperm.	29-X-1968	5000	52	0.78 ± 0.02 (20)	0.86 ± 0.03 (20)
S 75/12	Bonaire	partly covered well	-	perm.	17-XI-1975	24	59	0.63 - 0.88 (5)	0.83 - 1.09 (7)
S 80/42	Bonaire	open well	4.0	perm.	30-V-1980	60	53	0.86 ± 0.03 (11)	0.94 ± 0.04 (22)
S 75/14	Bonaire	open well	-	perm.	17-XI-1975	41	57	0.82 ± 0.02 (6)	0.89 ± 0.06 (17)
WH 886	Bonaire	open well	1.7	perm.	10-IX-1967	36	44	0.90 ± 0.03 (15)	1.06 ± 0.02 (22)
WH 887	Bonaire	open well near 886	2.2	perm.	10-IX-1967	395	61	0.93 ± 0.02 (11)	1.08 ± 0.03 (26)
S 75/15	Bonaire	partly covered well	0.8	-	17-XI-1975	109	111	0.82 ± 0.02 (21)	0.96 ± 0.04 (18)
S 75/16	Bonaire	well, roof collapsed	-	-	17-XI-1975	19	100	0.83 ± 0.03 (6)	0.93 ± 0.02 (6)
S 76/22	Bonaire	small holes in coral rock	0.8	-	14-VI-1976	54	35	0.84 ± 0.04 (13)	0.93 ± 0.04 (17)
WH 53e	Bonaire	pool	0.7	semiperm.	26-III-1955	125	87	0.87 ± 0.03 (15)	0.99 ± 0.03 (14)
WH 53i	Bonaire	pool	5.1	semiperm.	26-X-1968	54	54	0.93 ± 0.03 (12)	1.06 ± 0.02 (17)
WH 54f	Bonaire	pool	0.2	temp.	4-XII-1963	28	12	0.93 (3)	1.09 ± 0.02 (18)
WH 104Bc	Aruba	slowly overflowing pool	1.8	semiperm.	12-VIII-1955	61	47	0.81 ± 0.02 (18)	0.89 ± 0.02 (25)
WH 104Ab	Aruba	waterflow	1.8	semiperm.	12-VIII-1955	17	42	0.85 ± 0.02 (5)	0.96 ± 0.03 (12)
WH 103B	Aruba	pool	6.1	-	5-XI-1963	60	50	0.87 ± 0.03 (16)	0.99 ± 0.04 (32)
WH 103d	Aruba	brooklet	4.4	perm.	20-X-1967	39	86	0.89 ± 0.03 (18)	1.05 ± 0.03 (21)
WH 103	Aruba	brooklet	3.2	perm.	6-I-1937	27	31	0.90 ± 0.01 (5)	1.08 ± 0.02 (16)
S 78/294	Aruba	trickle	3.6	-	17-V-1978	7	-	0.87 (1)	0.97 ± 0.03 (5)
WH 66	Curaçao	pool	2.0	semiperm.	6-IX-1936	490	47	0.80 ± 0.02 (22)	0.93 ± 0.04 (33)
WH 539a	St. Martin	pool	0.7	temp.	29-VI-1955	100	33	0.85 ± 0.03 (22)	0.97 ± 0.03 (33)
WH 867	Barbados	pond	0.14	semiperm.	6-VII-1967	13	-	0.85 - 0.90 (2)	1.03 ± 0.03 (10)

ferences must cause the size difference. The same holds true for the brooklet WH 103 and the pool (WH 103B) next to it. Again there is no correlation with chlorinity. The size range of the animals in the samples from Aruba is about the same as in those from Bonaire.

On Curaçao, St. Martin and Barbados, *H. margaritae* has been encountered only once, in pools. In the wells of Curaçao a *Cypridopsis* species, which was found less frequently on Bonaire and Aruba, was predominant. Possibly *H. margaritae* is competitively excluded by this *Cypridopsis* species on Curaçao.

In only a single Paraguana sample the species is represented by more than a few specimens, of small size. On Grenada and on Tortugillo only a few specimens are found, like in many other stations on Bonaire, Aruba and Margarita, which are not included in table I.

Comparing the size differences between intra-insular samples, there is no indication of genetic isolation. There are size differences between the samples from Margarita, Los Testigos and La Blanquilla, which could indicate a geographic barrier and may point to some form of genetic isolation. However, in

these islands only a few large samples were taken, so this conclusion remains disputable. Furthermore, the size range within Bonaire is very large, and totally overlaps the ranges of all other islands.

Even in the same station in different years there are differences in length. Furthermore, the species seems perfectly capable of surviving dry periods by way of resistant eggs. Therefore it seems more probable that the size differences between the samples are influenced by differences in environmental factors. However, when size is compared with depth, area (size) of habitat, and chlorinity, by way of Pearson's product-moment correlation coefficient, no correlation is found (e.g. mean length males with chlorinity: $r = 0.047$, $p = 0.85$; mean length females with chlorinity: $r = -0.12$, $p = 0.57$).

When size differences are compared with coded environmental factors, a regression is found between area of habitat and mean length ($\sigma \sigma$: $r = -0.71$, significance level 0.002, $n = 16$; $\varphi \varphi$: $r = -0.44$, significance level 0.05, $n = 21$). There seems to be some correlation between area of habitat and carapace length, in which the animals tend to be larger in smaller waters.

Data are also compared by single classification analysis of variance, especially for the nonmetrical factors like habitat, soil etc. With area of habitat as well as permanency a low probability is found for males but not for females (for permanency: F probability ($\sigma \sigma$) 0.034, $n = 14$; ($\varphi \varphi$) 0.356, $n = 19$). Here too the number of observations is very small. Males tend to be smaller in permanent habitats.

There seems to be some correlation with environmental factors, but nothing conclusive can be said because the number of observations is very low for each combination. Multiway analysis of variance or multiple regression is not possible because there are not enough cases for which all environmental factors were measured.

3.3. *Heterocypris antillensis* (table II)

On Aruba the specimens from the covered well, S 78/291, are the smallest. The specimens sampled in 1948 and 1949 in the pond WH 401

are medium-sized. The animals from WH 636, a 1½ year old small cemented pool in a garden, are the largest. The number of Aruban sampling stations yielding this species is not sufficient to justify any conclusion.

On Curaçao the sampling stations with *H. antillensis* are all situated in the central part of the island, except for one in the north (WH 943). In WH 396, a temporary pool, three samples were taken at the same time in 1948, when there had been water at this station for only 2-3 weeks. Between the three samples the maximal size differences resulted in: $t = 3.16$ ($p < 0.01$) for females, and $t = 1.97$ ($p < 0.1$) for males. These reasonably large differences can not be explained and show with how much care the size differences have to be interpreted. Although the animals sampled in 1955 are somewhat smaller in size than those from 1948, the difference in length between the smallest animals from 1948 and the largest from 1955 is not statistically significant ($p > 0.1$). In WH 397, a semipermanent pool, the animals were larger in August 1948 and smaller in December 1948 and in 1955. The animals of the last mentioned samples have the same carapace length as those from the nearby pool WH 396d and as those from the temporary pool WH 943 in the north, sampled in 1970. WH 82, a dug, open well, was permanent in 1936 and not populated by *H. antillensis*. This well became semipermanent in 1949, dry for a few months each year, very shallow, and containing small-sized specimens of *H. antillensis*. The specimens from WH 895, a temporary pool, are large-sized and of the same length as those from WH 397.

On Klein Curaçao, in a semipermanent open well, the smallest *H. antillensis* were encountered.

On Bonaire the specimens from WH 376A, a sheet of rainwater, and from WH 805, a large semipermanent pool, have about the same size and are as large as the animals from WH 809, a sheet of rainwater on Klein Bonaire. The animals from WH 378, another sheet of rainwater near WH 376A (fig. 1) are much smaller ($p < 0.001$). S 76/33, an almost dry open well, contains the smallest animals of Bonaire. In

TABLE II

Mean carapace length, sex ratio, and some environmental data of the different samples containing *Heterocypris antillensis*. Sex ratio is defined as number of males per 100 females.

Station no.	Island or region	Type of habitat	Chlorinity (g Cl ⁻ /l)	Permanency	Date	N of specimens	Sex ratio	Carapace length	
								♂♂ mean ± S.D. (n)	♀♀ mean ± S.D. (n)
S 78/291	Aruba	covered well	0.3	—	16-V-1978	55	20	1.07 ± 0.05 (8)	1.21 ± 0.05 (40)
WH 401	Aruba	pond	0.0	semiperm.	30-XII-1948	107	16	1.14 ± 0.04 (12)	1.33 ± 0.05 (28)
WH 401a	Aruba	pond	0.0	semiperm.	18-I-1949	13	—	1.18 (1)	1.30 ± 0.03 (12)
WH 636	Aruba	pool	0.1	temp.	4-V-1955	53	51	1.23 ± 0.04 (9)	1.40 ± 0.04 (25)
WH 82a	Curaçao	open well	0.2	temp.	11-II-1949	209	27	1.09 ± 0.03 (30)	1.23 ± 0.03 (49)
WH 396(1)	Curaçao	pool, water since	0.3	temp.	20-VIII-1948	96	55	1.13 ± 0.04 (32)	1.30 ± 0.05 (62)
WH 396(2)	Curaçao	2-3 weeks	0.3	temp.	20-VIII-1948	40	25	1.14 ± 0.03 (8)	1.29 ± 0.05 (28)
WH 396(3)	Curaçao		0.3	temp.	20-VIII-1948	349	15	1.16 ± 0.04 (40)	1.28 ± 0.05 (40)
WH 396d(1)	Curaçao	pool	0.2	temp.	2-III-1955	34	36	1.09 ± 0.01 (6)	1.25 ± 0.03 (16)
WH 396d(2)	Curaçao	pool	0.2	temp.	2-III-1955	41	71	1.11 ± 0.04 (16)	1.26 ± 0.04 (20)
WH 397	Curaçao	pool	0.3	semiperm.	24-VIII-1948	90	23	1.17 ± 0.04 (14)	1.34 ± 0.05 (35)
WH 397a	Curaçao	pool	0.1	semiperm.	1-XII-1948	27	91	1.08 ± 0.05 (8)	1.26 ± 0.05 (8)
WH 397e	Curaçao	pool	0.2	semiperm.	2-III-1955	13	83	1.11 ± 0.05 (5)	1.28 ± 0.07 (6)
WH 895(1)	Curaçao	pool	0.3	temp.	26-X-1967	31	43	1.17 ± 0.07 (9)	1.35 ± 0.04 (19)
WH 895(2)	Curaçao	pool	0.3	temp.	26-X-1967	52	41	1.17 ± 0.03 (14)	1.34 ± 0.05 (29)
WH 943	Curaçao	pond	0.2	temp.	27-III-1970	145	41	1.11 ± 0.03 (33)	1.27 ± 0.03 (44)
WH 387	Klein Curaçao	open well	0.7	semiperm.	1-X-1948	45	15	1.06 ± 0.05 (6)	1.19 ± 0.05 (33)
WH 809	Klein Bonaire	sheet of water	0.1	temp.	3-XII-1963	37	64	1.30 ± 0.04 (12)	1.53 ± 0.05 (17)
S 76/33	Bonaire	almost dry well	0.2	temp.	15-VI-1976	44	45	1.13 ± 0.03 (12)	1.27 ± 0.06 (27)
WH 383	Bonaire	open well, type-locality	0.4	semiperm.	21-IX-1948	320	82	1.18 ± 0.03 (43)	1.34 ± 0.04 (40)
WH 378	Bonaire	sheet of water	0.2	temp.	24-II-1949	90	3	1.18 - 1.23 (3)	1.40 ± 0.06 (50)
WH 376A	Bonaire	sheet of water	0.1	temp.	3-IX-1948	16	100	1.29 ± 0.04 (8)	1.53 ± 0.04 (8)
WH 805	Bonaire	pool	0.7	semiperm.	6-XII-1963	120	34	1.30 ± 0.04 (16)	1.54 ± 0.05 (35)
WH 889A	Bonaire	pool	1.0?	temp.	22-IX-1967	120	65	1.36 ± 0.04 (28)	1.60 ± 0.04 (37)
WH 6	Araya	pool	0.4	temp.	27-VI-1936	42	86	1.19 ± 0.03 (16)	1.37 ± 0.05 (17)
WH 7	Araya	open well	0.5	temp.	27-VI-1936	24	26	1.20 ± 0.03 (5)	1.43 ± 0.08 (19)
WH 771	Martinique	puddle	2.0	temp.	11-II-1964	850	41	1.11 ± 0.03 (40)	1.28 ± 0.04 (51)
WH 673	Barbuda	water hole	1.0	temp.	10-VII-1955	500	67	1.32 ± 0.03 (27)	1.59 ± 0.03 (28)
WH 674(1)	Barbuda	pond	2.7	semiperm.	5-VII-1955	30	20	1.22 ± 0.04 (5)	1.38 ± 0.06 (21)
WH 674(2)	Barbuda	pond	2.7	semiperm.	5-VII-1955	16	—	—	1.45 ± 0.05 (15)
WH 674a	Barbuda	pond	4.0	perm.	21-VII-1967	24	14	1.21 - 1.24 (3)	1.42 ± 0.05 (18)
WH 676	Barbuda	pool	0.1	temp.	5-VII-1955	330	9	1.28 ± 0.03 (25)	1.51 ± 0.05 (30)
S 78/54	St. Martin	largely covered well	—	perm.	16-IV-1978	36	153	1.18 ± 0.04 (19)	1.35 ± 0.07 (12)
S 76/66	St. Martin	mostly covered well	2.6	perm.	23-VI-1976	19	46	1.11 - 1.13 (3)	1.33 ± 0.04 (12)
WH 094	St. Martin	pool	0.1	temp.	20-VII-1973	51	19	1.19 ± 0.03 (8)	1.36 ± 0.04 (39)
WH 095	St. Martin	pool	0.4	temp.	20-VI-1973	120	29	1.08 ± 0.05 (22)	1.33 ± 0.09 (36)
WH 097	St. Martin	pool	0.2	semiperm.	22-VII-1973	250	47	1.21 ± 0.04 (40)	1.46 ± 0.05 (45)
S 78/123	Virgin Gorda	open well	1.9	—	24-IV-1978	55	26	1.13 ± 0.03 (7)	1.34 ± 0.04 (36)
WH 707	Puerto Rico	pool	0.0	temp.	19-IX-1963	300	40	1.19 ± 0.05 (36)	1.35 ± 0.05 (43)

WH 889A, a small shallow pool, serving as a trough, the largest animals of Bonaire were encountered. Again it is very difficult to explain the size differences consistently. Sometimes the animals have different carapace lengths under similar circumstances, while in other stations which are very different, they have the same length.

The size range of *H. antillensis* on Bonaire is larger than that on Aruba, where it is larger

again than on Curaçao. So there is considerable overlap in carapace length between these islands. The two samples of the district Araya on the mainland of Venezuela contain medium- to large-sized specimens. Martinique, Virgin Gorda and Puerto Rico present one small- to medium-sized sample each.

Barbuda presents large animals. An inexplicable size difference between two samples taken the same day in WH 674 is encountered.

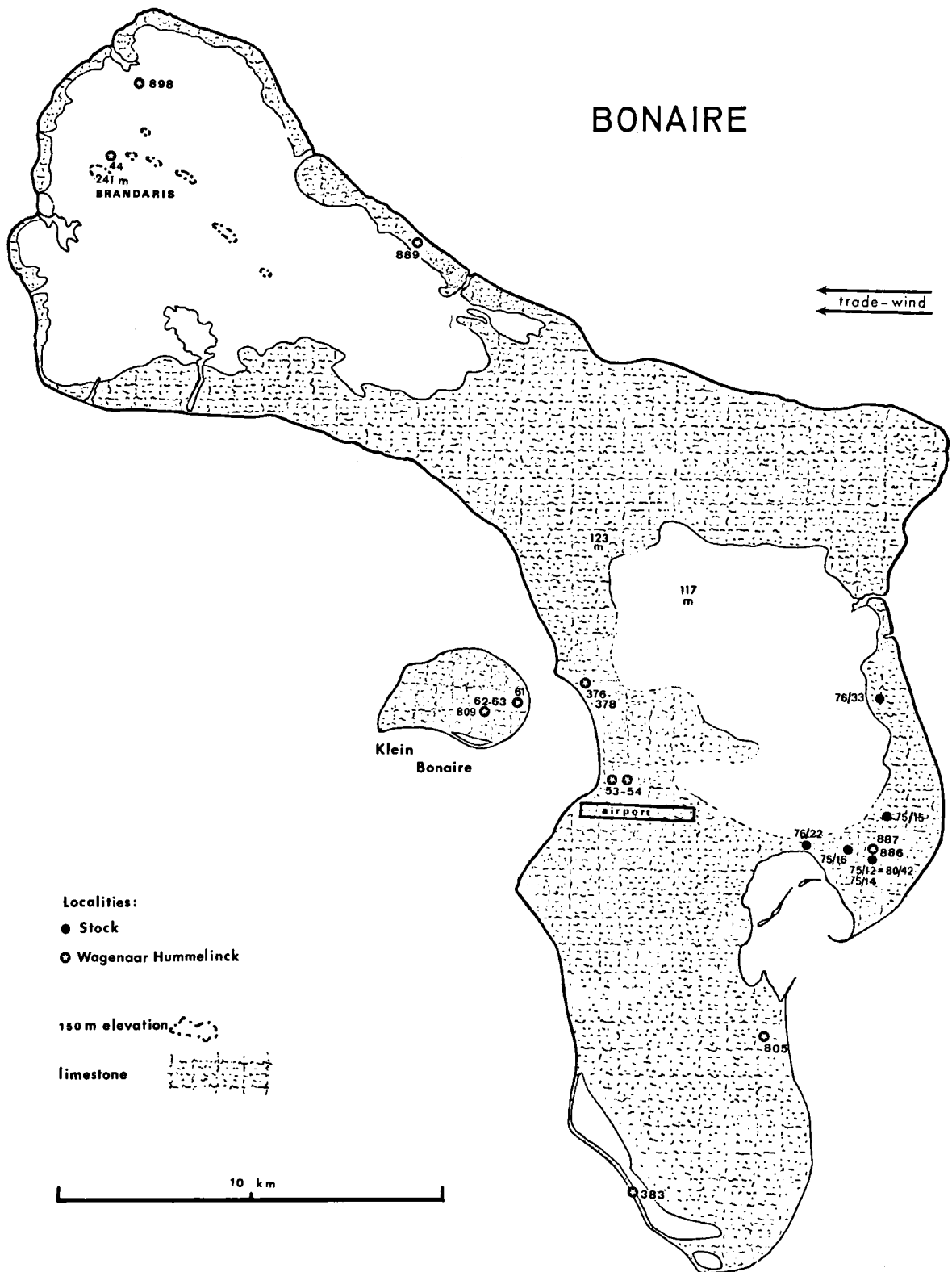


Fig. 1. Bonaire and Klein Bonaire, with station numbers of *Heterocypris* samples taken by Stock and Wagenaar Hummelinck.

There are considerable size differences between WH 673, a small, temporary, muddy, brackish water hole, containing large animals, WH 676, a larger, fresh, temporary pool, with smaller animals, and WH 674, the largest, semipermanent, muddy, brackish pool, with the smallest Barbudian animals. All stations are near each other. Here the environmental factors seem to affect carapace length.

St. Martin presents slight differences in length between S 78/54, a largely covered well, S 76/66, a partly covered well, both in the north, and WH 094, a temporary cattle pond in the south (fig. 2.). WH 095, a small temporary garden pool near WH 094, presents slightly smaller females ($t = 1.89$, $p > 0.05$), and males which are much smaller ($t = 6.99$, $p < 0.001$). In WH 097 the males are somewhat larger than in the afore-mentioned stations, but the females are very large ($t = 10.0$, $p < 0.001$). There is no indication of the cause of these size differences.

Comparison of the differences in carapace length between the islands (table III), reveals that on Bonaire the size range is very large, overlapping most of the size ranges of the species in all other islands. Curaçao presents small animals, Aruba small- to medium-sized animals and Bonaire medium- to large-sized animals. St. Martin presents small males, but females of medium length, and Barbuda presents large animals.

TABLE III

Range of mean carapace lengths at the various stations on each island for *H. antillensis*.

Island	♂ ♂	♀ ♀
Aruba	1.07-1.23 mm	1.21-1.40 mm
Curaçao	1.08-1.17 mm	1.25-1.35 mm
Bonaire	1.13-1.36 mm	1.27-1.60 mm
Barbuda	1.22-1.38 mm	1.42-1.59 mm
St. Martin	1.08-1.22 mm	1.33-1.46 mm

There are differences in carapace length between the islands which could indicate some degree of isolation, but on the other hand there is considerable overlap between the size ranges in the islands. Especially St. Martin, with its

comparatively large females in two of the samples, attracts attention (table III).

H. antillensis is almost never found in genuine covered wells, so nothing can be stated about differences in carapace length between populations from closed wells and open pools. In contrast with *H. margaritae* this species is mostly encountered in temporary waters, even in sheets of rainwater, often at low chlorinities. It seems that *H. antillensis* is a better colonizer of temporary habitats than *H. margaritae*. Both species colonize new habitats by way of resistant eggs transported by wind or animals. Therefore it is probable that most of the size differences can be explained by environmental factors rather than by some sort of genetic or geographic isolation of the different populations on the islands.

Like in *H. margaritae* no correlation is found between depth, area of the habitat, chlorinity, and carapace length. Even when these factors are divided in classes, no correlation is found. There seems to be a slight correlation between carapace length of males and the abundance of vegetation ($r = -0.45$, significance 0.052, $n = 19$), but this is less in females ($r = -0.35$, significance 0.15, $n = 19$). With single classification analysis of variance an *F* probability of 0.045 for male length, and of 0.06 for female length, with vegetation is established. The *F* probabilities found for all other factors with single classification analysis of variance are not significant. As in *H. margaritae* there are not enough combined data to perform a multiway analysis of variance or multiple regression. The only tentative conclusion can be that animals tend to be larger in habitats with little or no vegetation.

3.4. *Heterocypris punctata* (table IV)

Not many samples containing this species are available. On South Caicos only a few specimens have been found in an open well and a karst hole. It was never encountered in covered wells. The specimens with the smallest size are found in the samples S 82/08b, a small dug-out well on La Blanquilla, and WH 530, a cistern on St. Martin. In Barbuda the species

TABLE IV

Mean carapace length, sex ratio, and some environmental data of the different samples containing *Heterocypris punctata*. Sex ratio is defined as number of males per 100 females.

Station no.	Island or region	Type of habitat	Chlorinity (g Cl ⁻ /l)	Permanency	Date	N of specimens	Sex ratio	Carapace length	
								♂♂ mean ± S.D. (n)	♀♀ mean ± S.D. (n)
S 82/08b	La Blanquilla	open well, dug in clay	3.5	perm.?	19-II-1982	500	91	1.11 ± 0.02 (34)	1.21 ± 0.05 (40)
WH 667	Barbuda	sheet of water	2.2	semiperm.	9-VII-1955	23	77	1.17 ± 0.02 (10)	1.31 ± 0.04 (13)
WH 677A	St. Kitts	cattle pond well	1.5	temp.	20-VII-1955	2000	61	1.25 ± 0.05 (48)	1.40 ± 0.06 (60)
WH 677	St. Kitts	cattle pond	10.9	temp.	20-VII-1955	500	21	1.29 ± 0.05 (28)	1.48 ± 0.06 (31)
WH 527	Molly Beday (St. Martin)	puddle	0.8-1.0	temp.	3-VIII-1949	33	200	1.16 ± 0.03 (20)	1.36 ± 0.05 (10)
WH 528	St. Martin	pond	7.8	temp.	17-V-1949	710	69	1.22 ± 0.05 (93)	1.37 ± 0.06 (81)
WH 528b	St. Martin	pond	5.2	temp.	27-IX-1963	600	53	1.20 ± 0.03 (80)	1.32 ± 0.09 (74)
WH 530	St. Martin	cistern	9.9	semiperm.	18-V-1949	200	39	1.12 ± 0.03 (29)	1.22 ± 0.03 (47)
WH 610	St. Martin	land habitat near lagoon	—	—	27-VI-1955	3	—	—	—
WH 679	St. Martin	cistern	1.9	semiperm.	7-VI-1955	2	—	—	—
WH 545	Anguilla	overflowing puddle	5.0	semiperm.	18-VI-1949	3	—	—	—
S 79/145	South Caicos	open well	4.3	perm.	14-XI-1979	8	—	—	—
S 79/147	South Caicos	karst hole	0.2	—	15-XI-1979	1	—	—	—
Keyser (1975)	Florida (U.S.A.)		1.5-5.0	—	1975	—	—	1.08 - 1.14	1.23 - 1.32

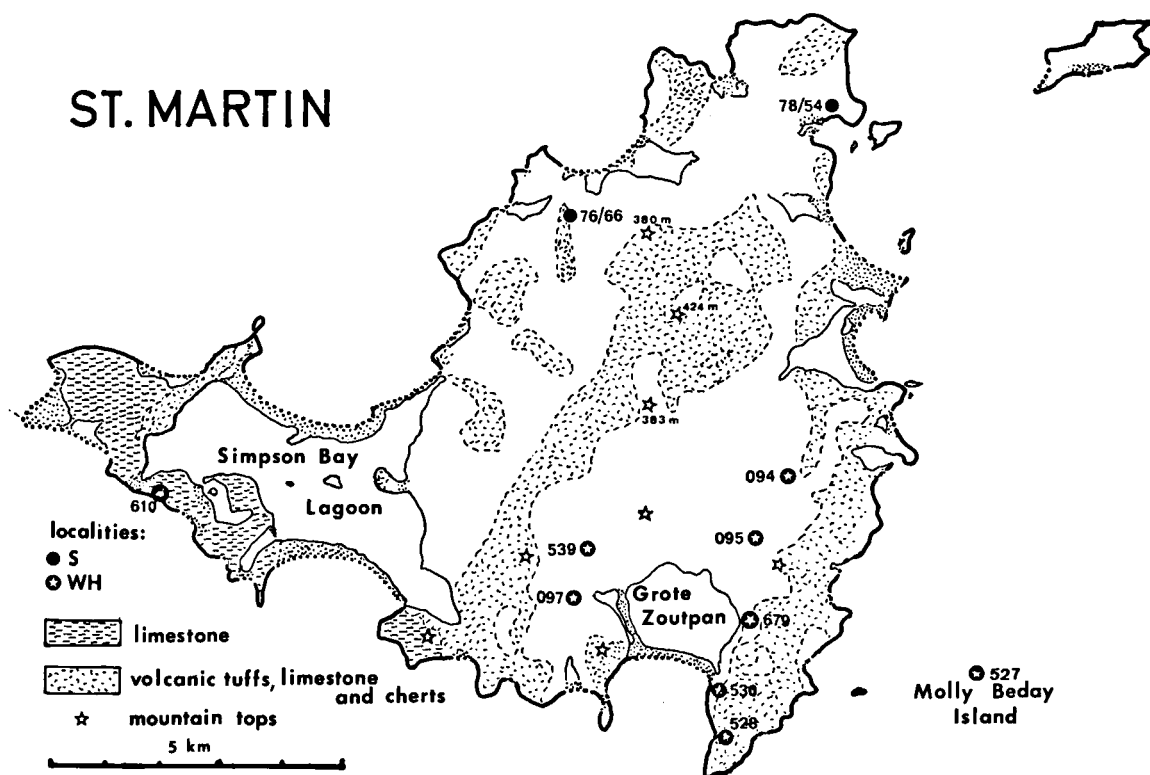


Fig. 2. St. Martin, with station numbers of *Heterocypris* samples taken by Stock and Wagenaar Hummelinck.

was encountered once in a large shallow sheet of rainwater (WH 667), with medium-sized animals.

In WH 528, a temporary pond in the south-west of St. Martin, two samples were taken, one in 1949 and one in 1963. There is a significant difference in length between the animals of these samples ($t(\sigma\sigma) = 3.13$, $t(\varphi\varphi) = 4.24$, $p < 0.001$). WH 530, a small cistern, is situated close to WH 528 (fig. 2), but the animals are much smaller ($p < 0.001$). WH 527, a small temporary puddle in solid rock, is situated on an islet about 3 km west of St. Martin. This sample contains medium-sized animals.

On St. Kitts there is a relatively large difference in length between animals from a cattle pond, WH 677, and from a well situated next to it, WH 677A, $t(\sigma\sigma) = 3.36$ ($p < 0.005$) and $t(\varphi\varphi) = 6.02$ ($p < 0.001$).

H. punctata probably colonizes new habitats with relative ease, like *H. antillensis*. It is encountered mostly in brackish waters, unlike *H. antillensis*, which is mostly dwelling in fresh and slightly oligohaline waters.

Again the differences in carapace length between various populations seem to be due to environmental factors rather than to genetic isolation in some form.

3.5. Discussion

One possible explanation for the size differences is that they are due to microevolution. When some of the populations are more or less isolated from each other geographically, they could develop their own special characters, without losing their ability to crossbreed with specimens from other populations, thus without becoming isolated genetically. Or, as Stanley (1979: 51) puts it: "In a typical species, gene flow may be sufficiently weak over long distances that clines and genetically distinctive clusters of populations are common, but sufficiently strong over short distances that successful speciation is rare". The latter seems to be the case in the present study. There are no clear differences in carapace length between wells and pools or other habitats, and there

seem to be some differences in carapace length between some of the islands. It seems that the species described in this paper can repopulate and colonize available habitats with relative ease. For *H. margaritae*, which is encountered more often in permanent habitats, isolation may be more easily established.

Furthermore, the differences in size between samples from the same wells and pools taken in different years can be as great of even greater than the size differences between different stations. Therefore it seems improbable that microevolution is the major cause of size differences between stations on the same island. Still, it may be possible that differences in carapace length between different islands are caused by microevolution, but this can not be proved with the data at hand. There are not enough samples from most of the islands and differences between other islands are either small or they overlap with differences between intra-insular samples. It seems more probable that the size differences are caused by changing or different environmental conditions.

Elofson (1941) suggested that differences in temperature may cause a variation in the size of ostracods. Szczechura (1971), after several years of breeding experiments with *H. incongruens* (Ramdohr, 1808), found "summer" and "winter" forms, i.e. a difference in size and shape caused by temperature fluctuations between the seasons. However, in the Caribbean, seasonal variations in temperature are only slight. So temperature does not seem to be the major cause of the variation in size as encountered in this study. Shallow pools or sheets of rainwater can get very hot by day ($> 40^\circ\text{C}$), while deeper wells have a more stable temperature ($27\text{--}29^\circ\text{C}$). Nevertheless, no correlation is found between carapace length and water depth. Neither is a correlation found between carapace length and most of the environmental factors measured in the field, such as soil, bottom, type of habitat, chlorinity, permanency, water colour and origin (i.e., natural or man-made). Only some correlation is found between carapace length and area of habitat in *H. margaritae*, and between carapace length and

vegetation in *H. antillensis*. But the number of data in these cases is very small. It is difficult to discover eventual correlations, as there are not enough samples from each separate island to compare the intra-insular size differences statistically with the accompanying environmental factors.

Smith (1965) found variations in size of adults of different cultured populations of *Chlamydotheca arcuata* (Sars, 1902). He believed that the temperature variation in the cultures was not significant enough to induce the size differences encountered in the different populations. Instead, he discovered that if there was more organic matter in the form of excretory products, the animals were smaller. When the animals were transferred to a clean tank they were larger after 5 or 6 generations. Rayment & Brännström (1962) found that specimens of *Cypridopsis vidua* (O. F. Müller, 1776), raised in either a calcareous or stagnant environment, were smaller than those raised under other conditions. Kaesler, in the discussion following the conference paper of Szczechura (1971) remarked that in 10 ponds within one drainage basin in Kansas (U.S.A.) probably statistically significant differences in size of adult *Cypridopsis vidua* were found. He concluded that size is correlated with parameters of water chemistry. McKenzie (1971) also found large size differences in different samples taken on the island Aldabra (East Africa, near Madagascar), of *Heterocypris giesbrechti* (Müller, 1898) and *H. symmetricus* (Müller, 1898). He found differences between covered and uncovered pools, and a relationship between length and salinity in *H. symmetricus*, but not in *H. giesbrechti*. Both species were larger in covered (i.e. more stable) pools. In an eight months culture of *H. giesbrechti* he found a seasonal variation in carapace length. However, McKenzie, in the discussion following Szczechura (1971), claimed that these variations were not temperature dependent and must in some way be affected by a combination of environmental conditions.

In *H. margaritae* and *H. antillensis* there is clearly no correlation between carapace length and chlorinity. Even comparison of intra-

insular samples results in a non-fit between carapace length and chlorinity. There is neither a correlation between carapace length and chlorinity in *H. punctata*.

Hartmann (1982) in a study with three species of littoral cytherid ostracods, found large variations in carapace ornamentation and size between different populations along the coast of Australia. He could not correlate this ornamental and size variation with any single environmental factor. His conclusion was that environmental and genetical influences play an integrated and complicated role in these variations between populations.

Juberthie et al. (1980) in a study on subterranean Coleoptera, found variation in length of limb segments and width of pronotum, between different populations. These biometrical variations were found within samples as well as between different samples. There was some correlation with altitude for part of the samples and some of the characters, but most biometrical variation could not be explained by simple ecological, geographical or climatic factors.

Still, the most probable cause of variation in carapace length between populations of *Heterocypris* species, must be some, or a combination of, environmental factors. Comparing the other publications on this subject, it is most probable that the variation is somehow influenced by food abundance or shortage, pollution with organic matter, and probably other factors of water chemistry. Some amount of genetic variation, especially between islands, can not be excluded.

Carson (1975) states that there are groups that speciate extensively and groups that do not. If this is true then it is probable that the species of *Heterocypris* studied in this paper belong to the latter group. He concludes that the latter group of species has extensive "open" genetic variability and that efficient dispersal and high vagility also contribute to a large "open" genetic system. It seems that the *Heterocypris* species described in this paper disperse with relative ease from island to island and from locality to locality. This could mean

that they have a large genetic variability, not leading to speciation, in agreement with Carson's postulation.

4. ECOLOGY

4.1. *Treatment of the data*

All environmental factors were divided in classes or types. For each of the *Heterocypris* species it was calculated how often it occurred in each class or type, in absolute figures and in percentages.

Since the majority of the samples with *H. margaritae* were from the islands Margarita, Bonaire and Aruba, all samples from these islands containing ostracods were treated in the same way. This resulted in tables for each environmental factor (tables V-VII), and made it possible to compare the number of samples containing *H. margaritae* with the total number of samples containing ostracods, in each class or type of environmental factor (in the respective islands). By means of a chi-square test it was determined whether *H. margaritae* was encountered significantly more or less frequently in some of the classes or types of environmental factors.

The same analysis was executed for *H. antillensis*, but in this case the islands Aruba, Curaçao, Bonaire and St. Martin were used as reference. Only a few samples with *H. punctata* were available, which made it impossible to compare data in the way done for the other two species.

4.2. *The environmental factors and the species*

Habitat (table V). — No statistically significant differences were found between the distributions of *H. margaritae* and *H. antillensis* in the different types of habitat, as compared with the expected frequencies in the respective islands. Both species were most frequently encountered in pools, ponds and wells (being types of habitat predominantly sampled). *H. margaritae* occurred in all types of habitat. *H. antillensis* was found in all karst holes sampled, and never in springs, trickles, cisterns and sink

holes. *H. punctata* was encountered in pools, ponds, cisterns and sheets of rainwater.

Soil (table V). — *H. margaritae* was encountered on all types of soil. Samples from limestone were most frequent, but as compared with all samples containing ostracods, it was found significantly less on limestone and more on other types of rock ($p < 0.05$). *H. antillensis* was encountered most frequently on limestone, the percentual distribution of the samples in the soil types being about the same as for all samples containing ostracods. Five of the ten stations with *H. punctata* were situated in limestone surroundings.

Bottom (table V). — Both *H. margaritae* and *H. antillensis* were found mostly on muddy bottoms. The percentual distribution in the various types of bottom is about the same as for all samples containing ostracods in the respective islands. *H. antillensis* was found somewhat more frequently on mud, and never on sand. *H. punctata* was encountered on mud and sandy mud.

Area and depth (table VI). — For area as well as for depth no significant differences in distribution in the various size classes were found, for none of the species. *H. antillensis* was encountered less frequently in waters deeper than 1.5 m, but the difference is not conclusive.

Chlorinity (table VII). — *H. margaritae* was encountered at chlorinities ranging from 0-14 g Cl/l. Compared with the percentual distribution of all samples containing ostracods in the chlorinity classes, *H. margaritae* was found somewhat more often at chlorinities of more than 1.5 g/l, and less at chlorinities lower than 0.25 g/l. However, these differences were not statistically significant. *H. antillensis* was encountered mostly at chlorinities of less than 1 g/l, but sometimes at chlorinities up to 4 g/l. It was found significantly more often in fresh and slightly oligohaline waters ($p < 0.05$). *H. punctata* was encountered mostly at higher chlorinities, but also in fresh waters. Keyser (1975) found it mainly in mesohaline waters.

TABLE V

Distribution of the *Heterocypris* species with respect to type of habitat, kind of soil, bottom, and origin of the habitat.

HABITAT	wet mud	sheet of water	pool, pond	basin	cistern	karst holes	sink- and bore holes	well	spring	trickle	total no. of samples	statistics
<i>H. margaritae</i>	— —	3 (6%)	23 (45%)	2 (4%)	1 (2%)	1 (2%)	3 (6%)	11 (22%)	3 (6%)	4 (8%)	52	$\varphi = 3$
All stations ¹⁾	1 (1%)	8 (6%)	68 (49%)	6 (4%)	3 (2%)	1 (1%)	5 (4%)	32 (23%)	6 (4%)	5 (4%)	138	$\chi^2 = 2.82$
<i>H. antillensis</i>	1 (2%)	4 (7%)	37 (62%)	2 (3%)	— —	6 (10%)	— —	10 (17%)	— —	— —	60	$\varphi = 3$
All stations ²⁾	1 (5%)	14 (6%)	127 (50%)	15 (6%)	14 (6%)	5 (2%)	13 (6%)	50 (20%)	11 (4%)	3 (1%)	255	$\chi^2 = 6.86$
<i>H. punctata</i>	— —	2 (18%)	5 (45%)	— —	3 (27%)	— —	— —	— —	1 (9%)	— —	11	

SOIL	lime- stone	concrete	cultivated soil	diorite	volcanic	rock detritus	schist	porphyrid	other type of rock	diabase	total no. of samples	statistics
<i>H. margaritae</i>	15 (39%)	3 (8%)	1 (3%)	4 (11%)	— —	2 (5%)	2 (5%)	2 (5%)	3 (8%)	6 (16%)	38 (n_1)	$\varphi = 3$
All stations ¹⁾ (n_1)	55 (57%)	8 (8%)	— —	7 (7%)	— —	6 (6%)	3 (3%)	6 (6%)	4 (4%)	7 (7%)	96 (n_2)	$\chi^2 = 8.64^*$
<i>H. antillensis</i>	28 (68%)	2 (5%)	2 (5%)	3 (7%)	1 (2%)	1 (2%)	2 (5%)	— —	— —	2 (5%)	41	$\varphi = 3$
All stations ²⁾	122 (65%)	17 (9%)	9 (5%)	10 (5%)	1 (5%)	3 (2%)	4 (2%)	6 (3%)	3 (2%)	14 (7%)	189	$\chi^2 = 4.75$
<i>H. punctata</i>	5 (50%)	1 (10%)	2 (20%)	— —	— —	1 (10%)	— —	— —	— —	— —	10	

BOTTOM	mud	mud & rocks	sandy mud	sand (& gravel) (& rocks)	pebbles, stone, rock	masonry	total no. of samples	statistics
<i>H. margaritae</i>	10 (27%)	10 (27%)	4 (11%)	4 (11%)	6 (16%)	3 (8%)	37	$\varphi = 4$
All stations ¹⁾	29 (31%)	28 (30%)	13 (14%)	6 (6%)	12 (13%)	6 (6%)	94	$\chi^2 = 1.38$
<i>H. antillensis</i>	30 (65%)	4 (9%)	5 (11%)	— —	4 (9%)	3 (7%)	46	$\varphi = 3$
All stations ²⁾	91 (47%)	34 (18%)	17 (9%)	16 (8%)	18 (9%)	18 (9%)	194	$\chi^2 = 6.48$
<i>H. punctata</i>	7 (70%)	— —	3 (30%)	— —	— —	— —	10	

ORIGIN	natural	man-made	total no. of samples	statistics
<i>H. margaritae</i>	14 (41%)	20 (59%)	34	$\varphi = 1$
All stations ¹⁾	41 (45%)	50 (54%)	92	$\chi^2 = 0.12$
<i>H. antillensis</i>	14 (41%)	20 (59%)	34	$\varphi = 1$
All stations ²⁾	80 (44%)	101 (56%)	182	$\chi^2 = 0.12$
<i>H. punctata</i>	7 (64%)	4 (36%)	11	

¹⁾ in islands with *H. margaritae*; ²⁾ in islands with *H. antillensis*; * = $p < 0.05$.

Light conditions (table VII). — Both *H. margaritae* and *H. antillensis* occurred in covered, partly covered and open habitats, *H. antillensis* only a few times in covered and partly covered habitats. Because most of the samples with the two species were from open habitats, no statistically significant difference in distribution

could be proved. *H. punctata* was never found in covered or partly covered habitats.

Permanency (table VII). — *H. margaritae* was found mostly in permanent habitats, *H. antillensis* and *H. punctata* mostly in temporary habitats. However, these differences were not

TABLE VI

Distribution of the *Heterocypris* species with respect to the dimensions of the water body.

AREA OF HABITAT	smaller than 0.15 m ²	0.16 m ² to 0.55 m ²	0.56 m ² to 2.05 m ²	2.05 m ² to 10 m ²	10 m ² to 25 m ²	25 m ² to 100 m ²	100 m ² to 500 m ²	500 m ² to 1000 m ²	more than 1000 m ²	total no. of samples	statistics
<i>H. margaritae</i>	—	1 (3%)	6 (16%)	15 (48%)	1 (3%)	7 (19%)	3 (8%)	3 (8%)	1 (3%)	37	$\phi = 3$
All stations ¹⁾	3 (3%)	4 (4%)	23 (23%)	29 (29%)	5 (5%)	14 (14%)	9 (9%)	5 (5%)	7 (7%)	101	$\chi^2 = 3.18$
<i>H. antillensis</i>	4 (8%)	2 (4%)	5 (10%)	15 (29%)	4 (8%)	5 (10%)	8 (16%)	4 (8%)	4 (8%)	51	$\phi = 6$
All stations ²⁾	8 (4%)	7 (4%)	27 (14%)	56 (30%)	14 (7%)	26 (14%)	31 (17%)	11 (6%)	8 (4%)	188	$\chi^2 = 3.94$
<i>H. punctata</i>	1	—	—	—	—	5	3	—	2	10	

DEPTH	less than 0.15 m	0.15 m to 0.44 m	0.45 m to 1.14 m	1.15 m to 1.55 m	1.55 m to 2.0 m	2.0 m to 5.0 m	deeper than 5.0 m	total no. of samples	statistics
<i>H. margaritae</i>	1 (3%)	10 (25%)	20 (50%)	4 (10%)	4 (10%)	1 (3%)	—	40	$\phi = 2$
All stations ¹⁾	9 (8%)	29 (26%)	42 (38%)	12 (11%)	11 (10%)	6 (5%)	1 (1%)	110	$\chi^2 = 2.67$
<i>H. antillensis</i>	5 (9%)	14 (25%)	28 (51%)	5 (9%)	2 (4%)	1 (2%)	—	55	$\phi = 4$
All stations ²⁾	22 (10%)	48 (22%)	92 (43%)	17 (8%)	14 (7%)	16 (8%)	5 (2%)	214	$\chi^2 = 4.53$
<i>H. punctata</i>	1 (9%)	3 (27%)	6 (55%)	1 (9%)	—	—	—	11	

¹⁾ in islands inhabited by *H. margaritae*; ²⁾ in islands inhabited by *H. antillensis*.

large enough to be statistically significant. Only for *H. antillensis* the probability of a difference was close to 0.05.

Water colour (table VII). — This is a parameter for pollution and/or algal growth. If the water is strongly coloured it does probably contain much organic matter in one form or another. *H. antillensis* was found significantly more often in habitats with strongly coloured water ($p < 0.005$). *H. margaritae* occurred more often in habitats with clear or slightly coloured water, but this difference was not large enough to be statistically significant. *H. punctata* was encountered in habitats with clear as well as with coloured water.

Origin (table V) and vegetation (table VI). — *H. margaritae* and *H. antillensis* were encountered both in natural and man-made habitats, and in waters with either much or no vegetation. No statistical significant differences were found. *H. punctata* was encountered mostly in natural waters with much vegetation (few data only).

4.3. The habitats for each species

H. margaritae dwells mostly in pools, ponds and wells of medium size, but sometimes in larger pools and deeper waters. It is a euryhaline species ranging from fresh to polyhaline conditions, which can live in habitats without light. It was found on all types of bottom and soil, somewhat less on limestone and more on other types of rock, like diabase and diorite.

H. antillensis occurs mostly in pools, ponds, karst holes and shallow open wells. It was encountered in wet mud and shallow sheets of rainwater. The area of the habitat is not important, it dwells in very small and very large water bodies with depths up to 1.5 m, preferring low chlorinities. It seems to tolerate chlorinities up to 4 g/l. The species was found mostly in temporary, slightly to strongly coloured or polluted, water bodies, with a muddy bottom on limestone soil.

Of *H. punctata* only 12 samples were available. The species was found in larger, uncovered water bodies, especially with higher chlorinities, on limestone with a mud or sandy mud bottom. However, in La Blanquilla a large

population was encountered in a small open well. Keyser (1975) found the species in oligo- to mesohaline waters on detritus and mud.

4.4. Conclusions and discussion

Clearly there are differences in the ecology of the three species. The species almost never occur together. Only a few samples with a small number of both *H. margaritae* and *H. antillensis* were found. At La Blanquilla two small dug-out wells only 3 metres apart were sampled; one of them relatively clean and still in use, contained many specimens of *H. margaritae* (S 82/08A), but the other one which was apparently not in use anymore, with numerous mosquito larvae, vegetation and more organic matter, contained many specimens of *H. punctata*. Regrettably enough only one water sample was taken (chlorinity: 3.5 g/l), but the chlorinity can not have differed too much for the two samples.

H. margaritae seems to be a species of more stable habitats of more or less oligohaline nature. On the other hand, *H. antillensis* seems to be a rapid colonizer of all kinds of water bodies of low stability, in particular cattle pools, most of the time with coloured, polluted water of low chlorinity. It is the more opportunistic of the three species, adapted to many fast-changing environmental factors except, probably, chlorinity. *H. margaritae* is able to survive in changing environments, but probably less so than *H. antillensis*. It is also possible that *H. margaritae* is less able to (re)colonize habitats after dry periods than *H. antillensis*. *H. antillensis* might produce more resistant eggs, which can survive dry periods longer, and also give the species better means to colonize or recolonize other habitats. However, laboratory experiments will be needed to prove differences in tolerance and abilities to survive extreme changes or other stress factors.

Another possibility explaining the habitat separation is that there is a strong competition between the three species. The fact that the species hardly ever occur together in one station seems to point in that direction. The problem of restricted space in wells and pools makes competition an important factor.

Hutchinson (1959) noticed that two related cohabiting species need to have a difference in body size which approximates the ratio 1 : 1.3. In *H. margaritae* and *H. antillensis* the size difference approximates this ratio. Still the two species almost never occur together. In this case the size difference does not seem to be sufficiently large to prevent strong competition.

It is most probable that a combination of ecological characteristics, along with the competitive abilities of the species, determine if one or the other species will win the competition at each station.

H. punctata seems to be the more mesohaline representative of this genus. The fact that three specimens of this species were encountered in one of the terrestrial habitats on St. Martin could indicate that it has strong colonizing abilities, just like the other species. It is possible that the competition between *H. margaritae* and *H. punctata* in oligo- or mesohaline waters is won in most cases by *H. margaritae*.

McKenzie (1971) found on the island of Aldabra two species of the genus *Heterocypris* comparable to *H. margaritae* and *H. antillensis*: *H. symmetricus* (Müller, 1898), a large species (males: 1.06-1.42 mm, females: 1.33-1.66 mm, 28-33 whorls of spines in the Zenker's organ), living in temporary rainwater rock holes; and *H. giesbrechti* (Müller, 1898), a small species (males: 0.79-0.89 mm; females: 0.92-1.09 mm, 18-21 whorls of spines in the Zenker's organ), living in permanent freshwater reservoirs. *H. antillensis* is the larger species in the Caribbean (males: 1.07-1.36 mm; females: 1.21-1.60 mm, 32-36 whorls in the Zenker's organ), being mostly encountered in temporary waters, while *H. margaritae*, the smaller species (males: 0.77-0.94 mm; females: 0.86-1.09 mm, 18-23 whorls of spines), was found mostly in more permanent habitats.

There is a striking coincidence between the two species from Aldabra and the two from the Caribbean. The species also resemble each other morphologically. Actually, we can reach the same conclusion as McKenzie (1971) did for his species. The entire complex of environmental influences determines the fitness of *H. antillensis* for the more temporary habitats and

TABLE VII
Distribution of the *Heterocypris* species with respect to other environmental factors.

CHLORINITY (g Cl ⁻ /l)	less than 0.25	0.26 to 0.50	0.51 to 1.0	1.01 to 1.5	1.51 to 2.0	2.01 to 2.5	2.51 to 3.0	3.01 to 3.5	3.51 to 5.0	5.01 to 7.5	7.51 to 10.0	10.01 to 13.5	total no. of samples	statistics
<i>H. margaritae</i>	7 (15%)	8 (17%)	9 (19%)	2 (4%)	7 (15%)	1 (2%)	3 (6%)	2 (4%)	4 (8%)	2 (4%)	1 (2%)	2 (4%)	48	$\varphi = 5$
All stations ¹⁾	36 (30%)	19 (15%)	26 (21%)	6 (5%)	11 (9%)	4 (3%)	5 (4%)	3 (2%)	7 (6%)	2 (2%)	1 (1%)	3 (2%)	123	$\chi^2 = 7.71$
<i>H. antillensis</i>	23 (45%)	11 (22%)	7 (14%)	4 (8%)	2 (4%)	2 (4%)	1 (2%)	1 (2%)	—	—	—	—	51	$\varphi = 4$
All stations ²⁾	65 (28%)	51 (22%)	51 (22%)	13 (6%)	14 (6%)	6 (3%)	7 (3%)	3 (1%)	8 (3%)	5 (2%)	4 (2%)	6 (3%)	233	$\chi^2 = 10.02^*$
<i>H. punctata</i>	1	—	1	—	1	2	—	1	1	2	1	1	11	

LIGHT CONDITIONS				VEGETATION				total			
open	partly covered	covered	total no. of samples	no	some	much algae more veget.	much veget.	total no. of samples	statistics		
<i>H. margaritae</i>	38 (81%)	4 (9%)	5 (11%)	8 (32%)	5 (20%)	8 (32%)	4 (16%)	25	$\varphi = 2$		
All stations ¹⁾	110 (84%)	10 (8%)	11 (8%)	22 (34%)	20 (31%)	12 (19%)	10 (16%)	64	$\chi^2 = 2.24$		
<i>H. antillensis</i>	53 (93%)	2 (4%)	2 (4%)	9 (29%)	10 (32%)	6 (19%)	6 (19%)	31	$\varphi = 3$		
All stations ²⁾	221 (90%)	15 (6%)	11 (5%)	51 (34%)	36 (24%)	34 (23%)	29 (19%)	150	$\chi^2 = 1.79$		
<i>H. punctata</i>	11	—	—	—	1	—	4	5			

WATER COLOUR				PERMANENCY				total			
clear	slightly coloured	strongly coloured	total no. of samples	permanent	semi- permanent	temporary	total no. of samples	statistics			
<i>H. margaritae</i>	10 (59%)	2 (12%)	5 (29%)	16 (50%)	8 (25%)	8 (25%)	32	$\varphi = 2$			
All stations ¹⁾	24 (50%)	4 (8%)	20 (42%)	43 (53%)	13 (16%)	25 (31%)	81	$\chi^2 = 2.26$			
<i>H. antillensis</i>	5 (15%)	8 (24%)	20 (61%)	11 (24%)	6 (13%)	28 (62%)	45	$\varphi = 2$			
All stations ²⁾	56 (44%)	26 (21%)	44 (35%)	72 (41%)	25 (14%)	80 (45%)	177	$\chi^2 = 5.92$			
<i>H. punctata</i>	4	3	3	3 (30%)	2 (20%)	5 (50%)	10				

¹⁾ in islands inhabited by *H. margaritae*; ²⁾ in islands inhabited by *H. antillensis*; * - $p < 0.05$; ** - $p < 0.005$.

that of *H. margaritae* for the more permanent habitats. However, competitive exclusion is most probably another very important factor. In one of McKenzie's species there was a correlation between carapace length and chlorinity. This species, *H. symmetricus*, normally lives from 0-2.3 g Cl-/l, but at one station the chlorinity could range up to 5.3 g/l. *H. antillensis* was mostly encountered at lower chlorinities, without apparent differences in carapace length under different salinity conditions. However, the experiments with *H. symmetricus* were performed at one station, while data for *H. antillensis* are derived from different stations, and could have been influenced by other environmental factors, of which chlorinity is only one. It is possible that studies with one population of *H. antillensis* or *H. margaritae*, with other factors except chlorinity kept constant, can give rise to other conclusions.

H. giesbrechti did not react with change of size in different salinities. It is possible that this species, like *H. margaritae*, is used to life at higher salinities and does not react to changes of it, while for *H. symmetricus* and *H. antillensis* it is a real stress factor.

5. ZOOGEOGRAPHY

5.1. Comparison with related species

The species most closely related to *H. margaritae* is probably *H. communis* Klie, 1940, from the northeastern part of Brazil. This species has the same type of carapace, male maxillary palps, penis, and a comparable female copulatory organ. The Zenker's organ has 22 whorls of spines, the female carapace is 0.98 mm long and the male carapace is 0.88 mm long, both lengths being comparable with those of *H. margaritae*. The terminal segment of the maxillary palp is 1½ times as long as wide, as in *H. margaritae*. According to the description of Klie (1940), the right valve is longer than the left valve, and the tuberculation of the right valve is absent or indistinct. This prompted Purper & Würdig-Maciél (1974) to place this species in

the genus *Hemicypris*. However, considering all other characters, I think it is more likely that this species belongs to the genus *Heterocypris*.

The species *H. ? cochabambaensis* Purper & Pinto, 1980, of the last interglacial period (Pleistocene) from Bolivia, could easily be identical with *H. communis* or *H. margaritae*. It could also be an ancestor of both species or a very closely related species. It has the same carapace shape and length (1 mm). The length-width ratio is about 2.65, which is considered too high a value for the genus *Heterocypris* by Purper & Pinto (1980). However, in *H. communis* the length-width ratio is about 2.9, which is even more. In *H. margaritae* it is 2.66, thus the same.

H. affinis Klie, 1930 and *H. hyalinus* Klie, 1930, both from Paraguay, are probably related to *H. margaritae*, but not as closely as the above-mentioned species. *H. similis* (Wierzejski, 1893) from Argentina, redescribed by Ramirez (1968), does not correspond much with any of the species mentioned in the present paper.

The carapace morphology and size of *H. nicaraguensis* Hartmann, 1959, from Nicaragua, is like that of *H. margaritae*, but the structure of the hemipenis and the maxillary palps are more like those of *H. punctata*.

H. putei (Furtos, 1936), from Yucatan (Mexico), is also intermediary. The female carapace is like that of *H. antillensis*, the male carapace like that of *H. margaritae*, but the structure of the hemipenis and of the maxillary palps is more like those of *H. punctata*.

There are some more species which seem to be closely related to *H. antillensis*. *H. fluviatilis* (Furtos, 1933) and *H. glaucus* (Furtos, 1933), both from Ohio (U.S.A.) have a comparable carapace morphology. *H. fluviatilis* has 31 and *H. glaucus* 26 whorls of spines in the Zenker's organ. The furca of *H. fluviatilis* is much like that of *H. antillensis*, in contrast with the furca of *H. glaucus*. *H. dentatus* (Sharpe, 1910), as described by Tressler (1954), from Nebraska, Texas and Tennessee (U.S.A.), has about the same carapace shape, same size and same male maxillary palps, but it differs in the number of whorls of spines in the Zenker's organ and the length of claws and setae of the furca.

H. dentatmarginatus (Baird, 1859), as described by Sars (1889), from Australia, seems to be related to *H. punctata*, as most of the internal structures as well as the shape of the carapace agree with it. Sars (1889) related his species to *H. salinus*, as did Keyser (1975) for *H. punctata*.

The designation of a specimen of *Heterocypris* from Yucatan to *H. symmetricus*, by Furtos (1936) was not accepted by McKenzie (1971). It is probably a specimen of *H. punctata* (see Broodbakker, 1982: 224).

Another species which seems to be very closely related to, if not identical with, *H. punctata*, is *H. newmexicoensis* (Ferguson, 1967), a species described from New Mexico (U.S.A.). Because of the very concise description of this species, it is impossible without access to the material to clarify its relationships. The shape of the carapace is approximately the same, and its surface is reticulated, just as in *H. punctata*.

Only recently a paper was published on a new species: *H. bogotensis* Roessler, 1982, from Bogotá, Colombia. Roessler (1982) gives a detailed description of all the limbs and the carapace. This species is strikingly similar to *H. punctata*, however, only females were encountered. The shape of the carapace is the same, as are the length and height of the valves (right valve: 1.43 mm; left valve: 1.46 mm; height 58 % of the length). Unfortunately the surface structure of the valves is not mentioned. The maxillary palp has the same proportions, the second antenna has about the same lengths of segments and swimming bristles, and the furca has a ratio of 50 % for s_a/G_a , 86 % for s_p/G_p and 70 % for G_p/G_a (in females of *H. punctata*: 58, 81 and 72 %, respectively). However, the seta of T 1: E III is about as long as E II (in *H. punctata* it is 65 % of the length of E II). All these measurements were made on the basis of the drawings in Roessler's paper.

This would mean that *H. bogotensis* is probably very closely related to *H. punctata*. The fact that no males of *H. bogotensis* were encountered could be explained by the habitat of this species, which is situated on an altitude of 2600 m, which means another climatic regime. It is well known that for some species of ostracods par-

thenogenetic populations occur in higher latitudes and bisexual populations in lower latitudes (see Hartmann, 1968, for a discussion of this problem).

The Pleistocene species of *Heterocypris* as described by Swain (1977) from North America, have carapace shapes similar to those of *H. margaritae* and *H. punctata*. Because of loss of details in carapace structure and the absence of internal parts, it is practically impossible to place these fossil species conclusively.

5.2. Zoogeography of the three species

H. margaritae has its main distribution in the islands along the coast off Venezuela, and in the Venezuelan coastal states of Falcon and Araya. It was only once encountered on the islands St. Martin and Barbados. These last-mentioned islands could have been populated relatively recently by introduction through man or birds. It seems improbable that other ways of passive dispersal have played a role, because the islands between St. Martin, Barbados and the mainland of Venezuela do not seem to be inhabited by this species. Furthermore, the predominant trade winds are directed here from northwest to southwest, which makes it difficult for northern islands to be populated by southern species. A way of dispersal in northern direction, is dispersion by waterbirds, flying from Venezuela over the Windward Islands and further northwest to Puerto Rico and Cuba, a dispersal route accepted for gastropods of the family Planorbidae by Baker (1945).

The species most closely related to *H. margaritae* seem to live in the northern part of South America. It is therefore highly probable that *H. margaritae* has originated somewhere in the north of South America.

The distribution of *H. antillensis* is more complicated. It is found on St. Martin and some neighbouring islands, on Puerto Rico, as well as on Curaçao, Aruba and Bonaire. Most species which seem related to *H. antillensis* live in North America. The species was not encountered in samples from Haiti, Cuba and the Bahamas. However, Dr. Wagenaar Hum-

melinck did not take samples in Haiti and Cuba, and very few samples in the Bahamas. Thus it remains possible that this species, mostly encountered in pools and ponds, was not found in these islands because these types of habitat were not sampled. In Cuba the species was not present in samples from exclusively subterranean habitats, collected by Dr. L. Botosaneanu in 1971 and 1973.

H. punctata is a common species in southern Florida (Keyser, 1975), while it was unfrequently encountered in the Caribbean Islands. It was not found in samples from Cuba and Haiti, and only twice in samples from South Caicos (south of the Bahamas), probably because in the more northern islands few or no samples have been taken in epigeal habitats. It was present in one sample from La Blanquilla, but not in the other islands near the coast of Venezuela. Harrison & Rankin (1976) mentioned *H. symmetricus* from St. Vincent, from estuarine habitats. These animals are probably *H. punctata*, like the *H. symmetricus* described by Furtos (1936) from Yucatan (see section 5.1).

All these records could mean that *H. punctata* is a species more widespread than is known right now. It could be possible that the species has originated in South America. Further research will be needed to give a definitive answer to the question of the distribution of the three *Heterocypris* species and their related forms.

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