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A natural hybrid of *Leuciscus cephalus macedonicus* × *Chalcalburnus chalcoides macedonicus* (Pisces, Cyprinidae) from Lake Volvi (Macedonia, Greece)

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A massive hybridization between *Leuciscus cephalus macedonicus* and *Chalcalburnus chalcoides macedonicus* has been recognized and studied by examining 67 specimens from Lake Volvi (Macedonia, Greece). The majority of meristic and other characters present an intermediate position in the hybrid (total hybrid index $Vh = 38{\cdot}37$). Nevertheless, the best expression of intermediacy is shown most clearly by the numbers of anal fin soft rays, lateral line scales and gill rakers, and also by the height of the dorsal fin and the length of the base of anal fin. Of the examined hybrid specimens, 92·5% were females. It seems that hybridization takes place during the reproduction period in the main streams flowing into the lake under special conditions which hinder the migration of the majority of the population of *C. chalcoides* from the lake to the breeding sites. It is suggested that individuals of *C. chalcoides*, which manage to arrive in these sites, mate with *L. cephalus*, the normal inhabitant of the streams, thus producing the hybrid.

I. INTRODUCTION

Hybridization is a widespread phenomenon in nature. In fishes, our knowledge is most advanced for the freshwater species, partly because hybrids are more frequent in fresh water than in the sea and because freshwater fish populations are better studied. It is also enhanced by the increasing interest in hybrids, and because the frequency of hybrids has considerably increased due to environmental changes. This is readily seen by comparing the number of publications concerning hybrids reported in the lists of Slastenenko (1957) and Schwartz (1972, 1981).

These lists do not report any hybrids of freshwater fishes in Greece. The only hybrid to have been reported in Greece is *Barbus albanicus* × *Barbus graecus*, described by Stephanidis (1939), based on a single specimen from the Acheloos river (Western Greece)*. The recognition of hybrids in a natural population is a reflection of the relatively good state of knowledge of the Eurasian fish fauna as well as of a more intensive scrutiny of unusual-looking fishes (Wheeler & Easton, 1978). This ' relatively good state of our knowledge ' of the freshwater fish fauna of Greece allowed us to recognize a massive hybridization between the endemic subspecies *Leuciscus cephalus macedonicus* Karaman, 1955 and *Chalcalburnus chalcoides macedonicus* Stephanidis, 1971 in Lake Volvi, as well as other hybrids which are now under study. Hybridization between *Leuciscus cephalus* and *Chalcalburnus chalcoides* and their subspecies seems to be rare or not so well studied, since it has been reported only a few times (in the Soviet Union, Berg, 1949; see also Slastenenko, 1957; Schwartz, 1972, 1981).

*A hybrid of *Alburnus alburnus* × *Rutilus rubilio* has recently been recognized by Crivelli & Dupont (1987) from Lake Mikri Prespa.

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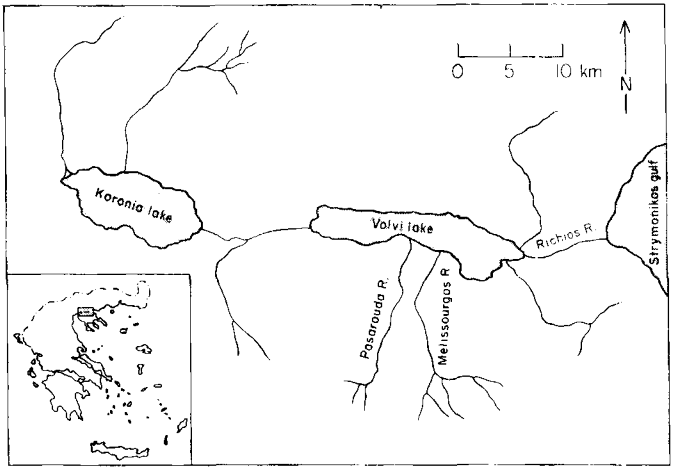

FIG. 1. Lake Koronia and Lake Volvi system.

II. MATERIALS AND METHODS

The hybrid was found in Lake Volvi, Macedonia (Fig. 1). Sampling was carried out from commercial catches. In two samples (21 September 1972 and 12 October 1972), 67 hybrid specimens (S.L. 157–208 mm) were found among *Chalcalburnus chalcoides macedonicus* and *Leuciscus cephalus macedonicus*. These specimens are deposited in the Zoological Museum of the University of Thessaloniki (ZMUT) (no. VA-70 and no. VA-71). Additionally, eight specimens (S.L. 163–184 mm) from the same samples are deposited in the National Museum of Natural History in Paris (MNHN) (no. 1975-731 and no. 1975-744). Ten more specimens (S.L. 162–204 mm) were collected in Lake Volvi on 20 and 30 October 1984 (ZMUT no. VA-81). Samples of the putative parental species were also obtained from the same lake.

Thirty-nine major characters were examined. Vertebral counts included the four vertebrae of the Weberian complex but excluded the urostyle. The last branched (soft) ray of the dorsal and anal fins was counted as two. Morphometric characters were measured to 0·1 mm with calipers, and are expressed as a percentage of standard length or head length. The mean ($\bar{x}$), standard error (Sx), standard deviation (s) and coefficient of variation (C.V.) were estimated. The hybrid index of Hubbs & Kuronuma (1943) was estimated according to the formula

$$Vh = \frac{1}{m} \sum_{i=1}^{m} (xhi - \mu 1i/\mu 2i - \mu 1i),$$

where xhi is the value of the character i for the hybrid h, $\mu 1i$ and $\mu 2i$ are the means for the character i in the parental populations 1 and 2, and m is the number of characters (Smith, 1973). For each character, the hybrid index may have values between 0 and 100. Negative values or 0 correspond to *Leuciscus cephalus macedonicus*, and values of 100 or more to *Chalcalburnus chalcoides macedonicus*. The ideal expression of intermediacy for a hybrid is the value 50, although index values between 30–70 are considered intermediate (Ross & Cavender, 1981).

Despite some disadvantages, the hybrid index provides a total impression of intermediacy, especially when allometry is avoided. The overall aim is to prove, through different ways, the real fact of hybridism, and towards this the hybrid index is undoubtedly of great importance. Some other qualitative morphological characters showing a remarkable intermediacy in the hybrid were also examined. The variability of a number of characters, and their intermediacy in the hybrid, are presented according to the method proposed by Hubbs & Perlmutter (1942) and Hubbs & Hubbs (1953). Examination of the gonads for sex determination was made macroscopically.

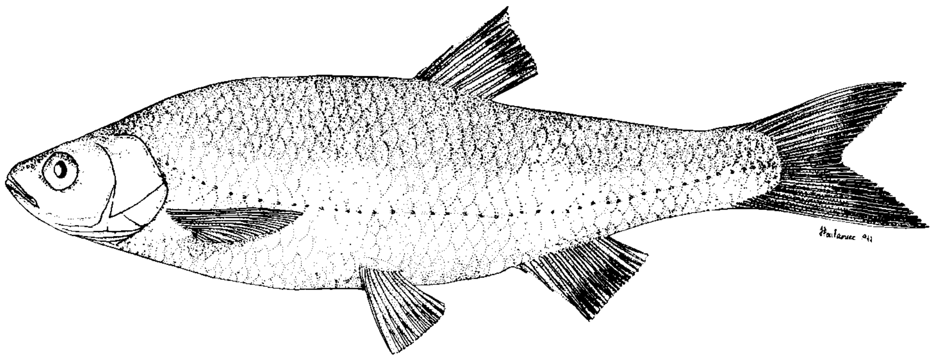

FIG. 2. *Leuciscus cephalus macedonicus* × *Chalcalburnus chalcoides macedonicus* hybrid from Lake Volvi, 225 mm S.L. (MNHN no. 1975 744).

III. RESULTS

The hybrid is known to the fishermen under the common name ' lakkopsaro ', meaning ' streamfish '. This name also characterizes *Leuciscus cephalus macedonicus* in the area, which resembles the hybrid (Fig. 2). However, examination indicates that the hybrid is distinguished by a thinner and higher body, and an anal fin with a straight margin and 10–11 branched rays (13 in one specimen only). On the other hand, in the shape of the snout and head, the hybrid resembles *C. chalcoides*. There are other characters which separate the hybrid from the two parental species and show it to be intermediate between them: of the 31 meristic characters and proportions of the body examined, 21 (68%) appear to have an intermediate expression in the hybrid (Tables I–III).

MERISTIC CHARACTERS

Five of the eight meristic characters are intermediate, one (type of pharyngeal teeth) is invariable, and two (rays of pectoral fin and vertebrae) show a greater average value in the hybrid than in the two parental species (Table I). The hybrid shows a greater range of values of branched rays in the pectoral fins. The number of vertebrae is clearly greater in the hybrid, both the average and extreme values. The other meristic characters have an intermediate value in the hybrid. Four of these (branched rays of anal and of ventral fins, gill rakers, and scales of the lateral line) are closer to *L. cephalus* (average hybrid index $Vh = 30{\cdot}25$) and only one (branched rays of dorsal fin) is closer to *C. chalcoides* ($Vh = 86$). The number of branched rays of the anal fin [Fig. 3(b)], the number of scales in the lateral line [Fig. 3(d)] and the number of gill rakers [Fig. 3(e)] show most clearly the intermediacy in the hybrid. In this last character, it is important to note that there is no overlap in extreme values, and the range of values of the hybrid is small relative to *C. chalcoides*. The same stability in values and their range is also observed in the branched rays of the anal fin [Fig. 3(b)] where the only divergence was due to a single specimen of the hybrid with 13 rays. There is some overlap in the extreme values of the number of scales of the lateral line [Fig. 3(d)] in the hybrid. The values are more stable in *L. cephalus* (5 scales), relatively stable in the hybrid (10 scales) and more variable in *C. chalcoides* (14 scales).

TABLE I. Meristics characters

Character	*Leuciscus cephalus macedonicus*					Hybrid					*Chalcalburnus chalcoides macedonicus*					Hybrid index
	n	$\bar{x} \pm S\bar{x}$	s	C.V.	Range	n	$\bar{x} \pm S\bar{x}$	s	C.V.	Range	n	$\bar{x} \pm S\bar{x}$	s	C.V.	Range	
Branched rays of dorsal fin	19	7·79 ± 0·10	0·42	5·38	7·00–9·00	67	8·03 ± 0·02	0·17	2·12	8·00–9·00	30	8·07 ± 0·05	0·25	3·14	8·00–9·00	86
Branched rays of anal fin	19	7·89 ± 0·07	0·32	3·99	7·00–8·00	67	10·52 ± 0·07	0·59	5·61	10·00–13·00	30	15·17 ± 0·14	0·79	5·22	14·00–17·00	36
Branched rays of pectoral fin	19	15·37 ± 0·14	0·60	3·87	15·00–17·00	67	16·19 ± 0·08	0·70	4·32	13·00–18·00	30	15·63 ± 0·11	0·61	3·93	14·00–17·00	100
Branched rays of ventral fin	19	8·21 ± 0·12	0·54	0·52	7·00–9·00	67	8·27 ± 0·05	0·45	5·44	8·00–9·00	30	8·67 ± 0·09	0·48	5·53	8·00–9·00	13
Scales of lateral line	19	45·21 ± 0·24	1·03	2·28	44·00–48·00	62	50·98 ± 0·29	2·30	4·51	47·00–58·00	17	61·65 ± 0·71	2·94	4·76	56·00–68·00	35
Gill rakers	10	9·50 ± 0·37	1·18	12·41	7·00–11·00	20	16·20 ± 0·21	0·95	5·86	15·00–18·00	16	27·81 ± 0·44	1·76	6·33	25·00–33·00	37
Vertebrae	10	42·50 ± 0·17	0·53	1·24	42·00–43·00	14	44·00 ± 0·23	0·88	2·00	43·00–46·00	16	41·44 ± 0·27	1·09	2·64	40·00–43·00	0
Radii of scale (anterior + posterior)	18	22·33 ± 1·63	6·93	31·02		10	17·70 ± 1·25	3·95	22·29		19	15·11 ± 0·79	3·46	22·92		64
Ratio of length:breadth of scale	18	0·88 ± 0·02	0·08	9·65		10	0·90 ± 0·02	0·05	5·76		19	0·72 ± 0·02	0·08	11·67		0
Pharyngeal teeth	10	5·2 – 2·5				19	5·2 – 2·5				16	5·2 – 2·5				
						1	5·2 – 1·5									
Average				7·82					6·43					7·35		41·22

TABLE II. Morphometric characters: dimensions (mm) and proportions of the body

Character	*Leuciscus cephalus macedonicus*					Hybrid					*Chalcalburnus chalcoides macedonicus*					Hybrid index
	n	$\bar{x} \pm S\bar{x}$	s	C.V.	Range	n	$\bar{x} \pm S\bar{x}$	s	C.V.	Range	n	$\bar{x} \pm S\bar{x}$	s	C.V.	Range	
Total length	19	199·77±8·64	37·66	18·85	137·4–277·2	67	222·21±1·31	10·75	4·84	196·0–257·0	30	199·26±3·54	19·40	9·74	168·3–238·0	—
Standard length	19	163·27±7·36	32·07	19·64	110·8–231·0	67	177·45±1·14	9·36	5·27	157·0–208·0	30	160·24±2·99	16·38	10·22	134·3–191·9	—
% of standard length:																
Body depth	19	24·04±0·24	1·06	4·41	22·28–26·66	67	25·16±0·12	0·99	3·93	22·70–27·87	30	22·66±0·15	0·83	3·68	20·95–24·74	0
Caudal peduncle depth	19	11·06±0·13	0·56	5·08	10·17–12·16	62	10·30±0·04	0·36	3·50	9·56–11·22	30	8·83±0·07	0·37	4·17	8·16–9·96	34
Caudal peduncle length	19	17·19±0·27	1·16	6·77	15·15–19·42	58	17·21±0·14	1·06	6·16	15·00–19·83	30	15·12±0·18	0·99	6·54	13·17–17·18	0
Head length	19	25·64±0·25	1·10	4·29	23·55–27·84	67	24·18±0·08	0·68	2·81	22·35–25·57	30	23·83±0·10	0·55	2·30	22·72–24·67	81
Horizontal diameter of eye	19	5·28±0·11	0·48	9·13	4·37–6·08	58	5·03±0·03	0·25	4·97	4·50–5·59	30	6·03±0·07	0·36	6·05	5·32–6·85	0
% of head length:																
Horizontal diameter of eye	19	20·54±0·34	1·49	7·24	17·50–23·40	58	20·81±0·15	1·15	5·53	18·82–23·66	30	25·30±0·24	1·31	1·29	23·02–27·49	6
Preorbital distance	19	32·22±0·34	1·48	4·58	29·11–34·84	59	29·78±0·27	2·11	7·09	27·00–42·44	30	30·82±0·22	1·23	3·98	27·66–33·41	100
Post-orbital distance	19	51·36±0·34	1·48	2·87	48·79–54·00	58	36·68±0·21	1·63	4·44	33·16–39·95	30	46·20±0·19	1·05	2·28	43·86–48·91	100
Interorbital width	19	36·62±0·38	1·66	4·53	34·60–39·69	65	34·28±0·16	1·28	3·73	31·43–37·25	30	29·18±0·22	1·23	4·21	26·88–31·4	31
Average				5·43					4·68					3·83		39·11

TABLE III. Morphometric characters: position and size of the fins (measurements in mm)

% of standard length	*Leuciscus cephalus macedonicus*					Hybrid					*Chalcalburnus chalcoides macedonicus*					Hybrid index
	n	$\bar{x} \pm S\bar{x}$	s	C.V.	Range	n	$\bar{x} \pm S\bar{x}$	s	C.V.	Range	n	$\bar{x} \pm S\bar{x}$	s	C.V.	Range	
Predorsal distance	19	54·78±0·27	1·16	2·11	52·77–57·04	67	55·03±0·13	1·07	1·94	52·22–57·61	30	56·32±0·21	1·17	2·07	53·42–58·32	16
Height of dorsal fin	19	19·27±0·24	1·06	5·52	17·50–21·33	60	18·47±0·11	0·88	4·76	16·97–20·18	30	17·25±0·14	0·78	4·52	15·22–18·51	40
Length of dorsal base	19	11·82±0·16	0·69	5·83	10·50–12·99	60	11·38±0·06	0·50	4·39	10·00–13·09	30	11·06±0·11	0·58	5·28	9·86–12·35	58
Height of anal fin	19	16·51±0·23	1·02	6·18	14·99–18·04	60	14·09±0·08	0·62	4·40	11·88–15·39	30	13·30±0·15	0·81	6·11	11·79–15·19	75
Length of anal base	19	9·82±0·18	0·76	7·79	8·21–11·41	60	12·21±0·08	0·60	4·91	11·16–13·74	30	16·10±0·12	0·66	4·13	15·11–17·89	38
Length of caudal fin	19	23·82±0·39	1·69	7·09	20·00–26·21	60	25·01±0·18	1·42	5·68	21·87 28·62	30	26·56±0·21	1·16	4·37	24·22–28·98	43
Length of pectoral fin	19	18·11±0·18	0·76	4·23	16·78–19·79	60	18·41±0·10	0·81	4·40	16·37–20·36	30	19·41±0·15	0·84	4·32	17·87–21·35	23
Length of ventral fin	19	15·28±0·15	0·64	4·19	14·22–16·63	58	14·39±0·07	0·54	3·75	13·39 15·95	30	14·49±0·11	0·59	4·05	13·28–15·52	100
Distance P-V	19	28·84±0·30	1·30	4·50	27·04–31·88	66	28·15±0·14	1·12	3·98	25·47–31·29	30	25·46±0·15	0·82	3·21	24·09–27·30	20
Distance V-A	19	23·07±0·23	1·00	4·33	21·28–24·50	65	22·98±0·12	0·97	4·22	20·65–25·89	30	21·57±0·16	0·89	4·12	19·73–23·42	6
Preventral distance	19	52·67±0·28	1·20	2·27	50·58–54·63	67	52·56±0·15	1·23	2·34	49·71–55·78	30	49·09±0·13	0·71	1·44	47·77–50·74	3
Preanal distance	19	74·03±0·32	1·38	1·87	71·66–76·75	67	73·78±0·14	1·14	1·55	71·79 77·02	30	69·54±0·21	1·16	1·67	67·76–72·28	6
Average				4·66					3·86					3·77		35·67

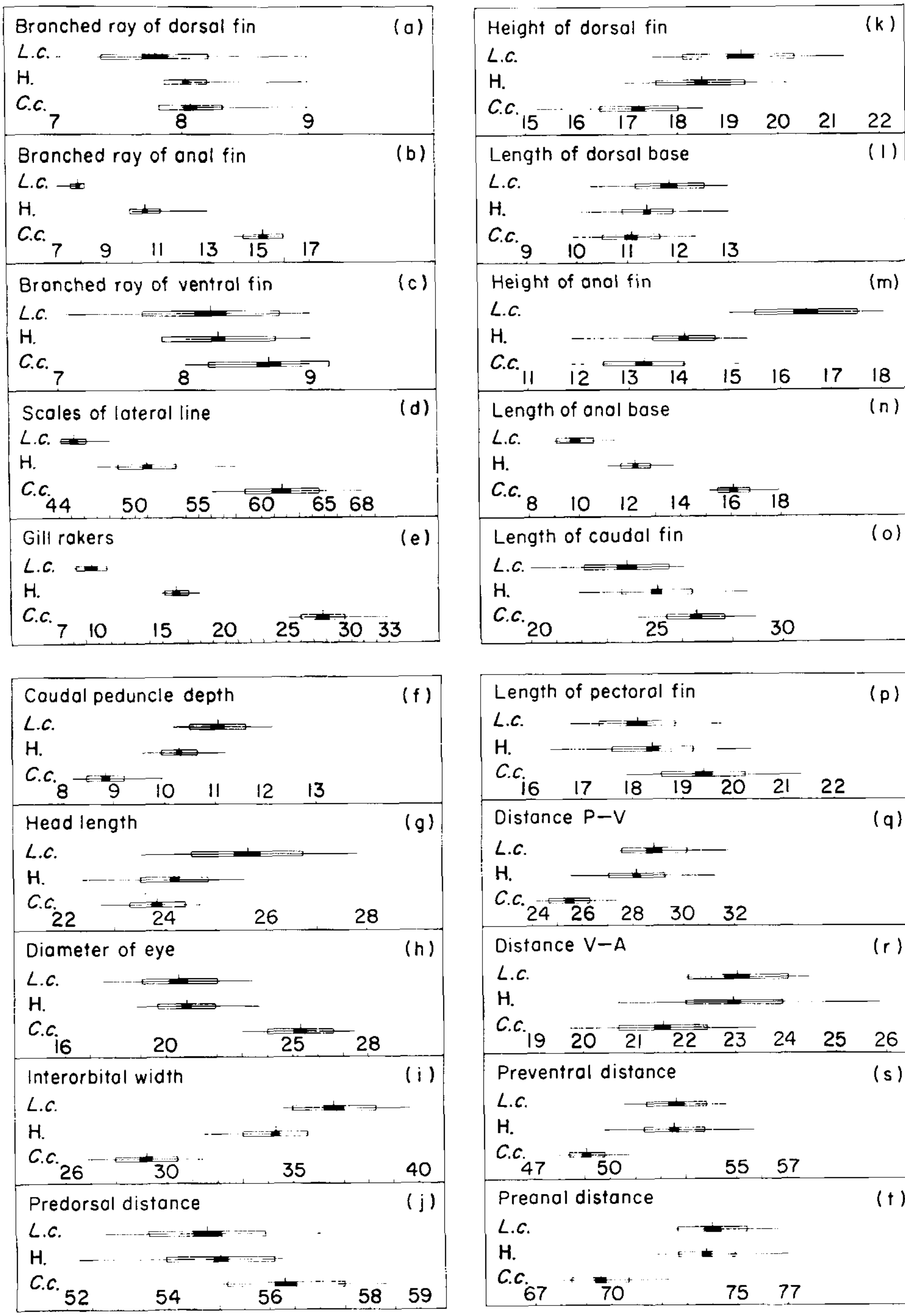

FIG. 3. Meristic (a)–(e) and morphometric (f)–(t) characters showing hybrid (H) intermediacy between parental species (*L.c.*, *Leuciscus cephalus macedonicus*; *C.c.*, *Chalcalburnus chalcoides macedonicus*). Range (horizontal line), mean (vertical line), one S.E. (black bar) and one S.D. (clear bar) on each side of the mean. Horizontal axis units are counted numbers for meristic characters and percentages for morphometric characters. Values are based on data in Tables I–III.

MORPHOMETRIC CHARACTERS

The hybrid has a medium-sized body, greater than the two parental species, at least of those examined (Table II). This applies especially to *C. chalcoides*, as this species rarely reaches a total length of 250 mm. However, *L. cephalus* reaches a greater size in other freshwater ecosystems of Greece, but in Lake Volvi fishing mortality probably causes a lack of larger specimens. Consequently, we cannot prove that the hybrid shows heterosis. However, the fact that the specimens of the hybrid and those of the two parental species are almost of the same size indicates that the other proportions of the body are apparently comparable, without any difficulties from allometry. Therefore, Table II shows that the hybrid has greater body depth and slightly greater caudal peduncle length than *L. cephalus*, and clearly greater than *C. chalcoides*, and a small eye, preorbital distance and post-orbital distance. These two last characters show a coefficient of variation (C.V.) almost twice as large as those of the two parental species, indicating greater variability. The other four proportions of the body (depth of caudal peduncle, head length, eye diameter and interorbital distance) have intermediate values in the hybrid. Of these characters, only head length is closer to *C. chalcoides* ($Vh=81$), the other three being closer to *L. cephalus*. The total hybrid index for these nine proportions of the body presents an intermediate value, $Vh=39{\cdot}11$ (Tables II, V). However, it is evident that this group of characters does not express the intermediacy very well, because five of them (55·6%) are with $Vh=0$ or 100.

The 12 characters which determine the position and size of fins (Table III) are mostly intermediate, with average $Vh=35{\cdot}67$. The only exception is the length of the ventral fins, which are smaller in the hybrid. Nine characters were closer to *L. cephalus* (average $Vh=21{\cdot}67$) whilst only length of base of dorsal fin and depth of anal fin were closer to *C. chalcoides* ($Vh=66{\cdot}5$).

The best expression of intermediacy is the height of the dorsal fin [Fig. 3(k)] ($Vh=40$) and length of the base of the anal fin [Fig. 3(n)] ($Vh=38$). In the latter character there is almost no overlap in the ranges of values, as is also the case with the numbers of the branched rays of the anal fin [Table I, Fig. 3(b)].

OTHER CHARACTERS

Many qualitative characters of the hybrid show a remarkable intermediacy (Table IV): the colour pattern of the body and fins, and the pigmentation of the peritoneum, are in intermediate positions, as are the free margin of the anal fin and position of the dorsal fin. The form of the snout and the orientation of the mouth resemble *C. chalcoides*, whilst the form of the keel resembles *L. cephalus*.

COEFFICIENT OF VARIATION AND HYBRID INDEX

The hybrid shows a mean coefficient of variation of 4·99 (Table V), not significantly different from those of the parental species. In the morphometric characters, the coefficient of variation of the hybrid is between that of the parental species, whereas for the meristic characters it is clearly smaller.

The total hybrid index is $Vh=38{\cdot}37$ (Table V). The closest to the ideal state for hybridization appears in the average index of the meristic characters ($Vh=41{\cdot}22$), but the index for the other characters is also close to intermediacy. However, the average hybrid index, in all cases, is smaller than 50, which indicates that the hybrid is more similar to *L. cephalus* than to *C. chalcoides*.

TABLE IV. Some significant qualitative characters showing an intermediacy in hybrid

Character	*L.c. macedonicus*	Hybrid	*C.c. macedonicus*
Free margin of anal fin	Convex	Straight	Concave
Peritoneum	Homogeneous, dark brown	Spotted, light brown	Spotted, light
Mouth	Terminal	Sub-dorsal	Dorsal
Snout (dorsal view)	Rounded	Intermediate	Angular
Abdominal keel	Absent	Small, often existing in front of the anus	Well developed
Pigmentation in anal fin	Dark in margin	Sparse	Without pigmentation
Pigmentation in scales at the sides of the body	Peripheric	More or less periferic or absent	All over the surface or absent
Pigmentation in cheeks	Well visible	Scarcely visible	Scarce or absent
Distance between insertions of dorsal and anal fins	One-third of the dorsal base	One-half of the dorsal base	Three-quarters of the dorsal base

TABLE V. Coefficients of variation and hybrid index of Hubbs & Kuronuma

	L.c. macedonicus	Hybrid	*C.c. macedonicus*
Coefficients of variation:			
(*A*) Dimensions and proportions of body	4·43	4·68	3·83
(*B*) Position and size of fins	4·66	3·86	3·77
Average *A* + *B* (morphometric)	4·54	4·27	3·80
(*C*) Meristic	7·82	6·43	7·35
Average *A* + *B* + *C*	5·64	4·99	4·98
Hybrid index:			
(*A*) Dimensions and proportions of body	—	39·11	—
(*B*) Position and size of fins	—	35·67	—
Average *A* + *B* (morphometric)*	—	37·14	—
(*C*) Meristic	—	41·22	—
Average *A* + *B* + *C* (Total index)*	—	38·37	—

*Calculation for all characters from 0 to 100.

SEX RATIO

In the hybrid, the dominance of the females over males is significant: of the 67 specimens of the hybrid, 62 (92·5%) were females, so the female:male ratio was 12·4:1. This great divergence from 1:1 indicates some abnormality, and provides additional proof of the identity of the hybrid and an indication of its possible sterility.

IV. DISCUSSION

Fish hybridization is favoured by genetic factors such as compatibility of genes (Dubois, 1981), simple reproductive behaviour (Pépin *et al.*, 1970), and ecological factors such as coincidence (in space and time) of reproduction (Hubbs, 1955). In cyprinids, these conditions are met to a significant degree, so that the hybrids are not very rare. This fact sometimes makes the criteria of separation of typical genera within this group doubtful (Pepin *et al.*, 1970). However, in nature, hybridization is usually not a very extensive or massive phenomenon. This preserves the autonomy of natural fish populations and justifies the maintenance of traditional nomenclature. Under natural conditions genetic incompatibility produces various blocks affecting the viability and fertility of hybrids (Hubbs, 1961) so that hybrids are often degenerate and parental populations can be maintained.

Hybridization can be increased in some cases, such as by the introduction of a species into an aquatic system where very closely related species live (Daget & Moreau, 1981), or where the environment is changed either through natural causes or by man (Hubbs, 1955). We believe that the massive hybridization between *Leuciscus cephalus macedonicus* and *Chalcalburnus chalcoides macedonicus* in the Lake Volvi system may be attributed to the latter.

The recognition of this hybrid was difficult at first; because a large number of adults were found, they gave the impression of an undescribed *Leuciscus* species. Besides the 67 individuals caught in two temporally close samples, the hybrid was fished for a long time before and after, so that its population in the lake was large.

An earlier faunistic study (Economidis & Sinis, 1982) left open the question of whether it was a new *Leuciscus* species or a hybrid. Even after the analysis of characters showed significant intermediacy (in comparison with the supposed parental species) (Economidis & Sinis, 1986), the problem of the presence of a large number of individuals raised the question: was such a massive hybridization possible in the balanced lake system of Volvi?

Leuciscus cephalus and *C. chalcoides* may coexist during the breeding season in streams flowing into the lake, especially those of Pasarouda and Melissourgos. *L. cephalus* is a rheophilous species with an important population remaining almost continuously in these streams, where they also breed. *Chalcalburnus chalcoides* is more limnophilous, and forms an important exploited population in Lake Volvi. In the past, this species migrated massively to breed in the streams. In the area, there are traditions and ancient texts which refer to the great size and density of migrating shoals. Athenaeus (second–third century A.D.) wrote: " Round Apollonia, in the Chalcidic peninsula, flow two rivers, the Sandy and the Olynthiac. Both empty into Lake Bolbe [=Volvi]. On the Olynthiac is a monument to Olynthus, the son of Heracles and Bolbe. In the months Anthesterion and Elaphebolion, so say the inhabitants, Bolbe sends the broiler to Olynthus, and at this time a limitless quantity of fish go up from the lake into the Olynthiac river. Now it is a stream so shallow that it hardly covers the ankle, nevertheless such a quantity of fish comes that all the inhabitants round about can put up preserved fish sufficient for their needs." Nowadays, this migration tends to be interrupted, due to increased agriculture and urbanization resulting in reduction of the water volume of the streams. The population of *L. cephalus* still remains in the streams, whereas migration of *C. chalcoides* from the lake is hindered by small irrigation dams along the streams. Migration of *C. chalcoides* is possible only during years with high rainfall in spring (mostly April). Thus, reproduction of this species sometimes coincides in time and space with that of *L. cephalus*, producing conditions for massive hybridization. Breeding sites are of small area with clear running shallow water and gravel bottom, because both species are lithophilous (Balon, 1975). Consequently, gamete-mixing of the two species occurs, as happens with other species breeding in rivers (Hubbs, 1955; Ross & Cavender, 1981). It seems that single individuals of *C. chalcoides* mixing with the spawning *L. cephalus* play an important role in the massive hybridization. This is similar to cases of hybridization reported in southern U.S.A. (Hubbs, 1955), Italy (Bianco, 1982), Portugal (Collares-Pereira & Coelho, 1983) and even those where special breeding conditions are required (Holčik, 1977).

There are strong indications that the hybrids are produced by female *L. cephalus* and male *C. chalcoides*. The hybrids mostly resemble *L. cephalus*, the total hybrid index, $Vh = 38{\cdot}37$ (Table V), being closer to *L. cephalus*. The females of *L. cephalus* are resident in the stream and better adapted to the environment so that solitary males of *C. chalcoides* preceeding the females in ascending streams meet females of *L. cephalus* at the breeding areas.

Berg (1949) has also described hybridization between *L. cephalus* and *C. chalcoides* based on intermediate characters, but these were not reported in detail. Howes (1981) rejected that example: " as enumerated, these characters could well describe a populational variant of one of the presumed parental species ". In Lake Volvi, however, it is clear that this hybridization exists. Otherwise, it is difficult to explain the stable occurrence, in a large sample of 67 fish, of 10–13 branched rays in the anal fin, while *L. cephalus* and *C. chalcoides* are known in the same lake system to have almost invariably 7–8 and 14–17 rays, respectively. Thus, the hybrid coexists with typical forms of the two parental species and cannot simply be rejected as a variant of either.

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