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Research Institute for Crop Production, Praha Ruzyně

**MELANISM IN POPULATIONS OF PHILAENUS SPUMARIUS (HOMOPTERA
APHROPHORIDAE) IN CZECHOSLOVAKIA**

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Abstract: The proportion of 11 colour morphs was investigated in 63 local populations of *P. spumarius* in Czechoslovakia, with particular respect to the ratio of light to dark forms. In total sample there were 83 % of light forms (*populi*, *typicus*, *trilineatus*) and 17 % of dark forms (8 other morphs). In dark forms females prevailed over males, while in the light form *populi* males largely outnumbered females. In local populations there were up to 51.6 % of melanic. Melanic populations were found in Carpathian mountains of northern and eastern Slovakia. The proportion of melanic was not correlated with altitude, or degree of environmental pollution of the sampling site.

Philaenus spumarius (L.) is a species with conspicuously polymorphic body coloration. The adults differ in pattern, hue, and saturation of the coloration of nearly all parts of body surface. The colour morphs are usually defined on the basis of colour patterns of dorsal side of the body (head, pronotum, scutellum, and forewings), but the individuals differ also in coloration of other parts of the body (Beregovoy, 1970, Svala and Halkka, 1974). Some 12—14 colour morphs could be distinguished in populations of Europe and North America (Farish, 1972, Halkka et al., 1973). In the design of morphs prevail either light, yellowish or brownish colour (light forms), or dark, grey to black colour (dark, melanic forms). The polymorphism proved to be heritable, being determined by a series of allelic genes whose expression and penetrance depends on non-allelic modifiers (Halkka et al., 1973). Morph proportions in contiguous populations of mainland areas with uniform conditions are characteristic, temporary stable and probably balanced by selective forces, while isolate marginal populations may be influenced by random genetic drift (Halkka et al., 1967, 1974a, b, c.f. Beregovoy, 1972). There exist clinal variation in proportions of different morphs, correlated perhaps with climatic differences (Farish and Scudder, 1967, Whittaker, 1972, Halkka et al., 1975). Local deviations in population composition may be caused by morph-specific food requirements of larvae (Halkka and Mikkola, 1977).

In most European populations light forms prevail over dark ones. Melanic populations were discovered in small areas at British Isles (Lees et al., 1983) and at high altitude localities of the western Ukraine (Halkka et al., 1980). We analyzed the structure of a number of Czechoslovak populations from localities which differed with respect to geographic position, altitude and degree of industrial pollution.

MATERIAL AND METHODS

Adults of *P. spumarius* were sampled in 1976—1983 at 63 localities of Czechoslovakia. The localities were between 47°50' and 50°55' N, and 12°40' and 22°35' E, at 130—1,200 m altitude. Most samples from high altitudes were collected in the Carpathian mountains of Slovakia. The

material was collected in June—September by sweeping from various herbaceous plant stands, both on road side vegetation polluted by automobile exhausts, and at unpolluted areas such as mountain meadows. Suitable host plants were: *Artemisia vulgaris*, *Geranium pratense*, *Chamaenerion angustifolium*, *Senecio nemorensis*, *Hypericum* sp.

The material was classified into 11 colour morphs according to Halkka et al. (1973). We accepted this simplified classification for the sake of comparability. There were distinguished

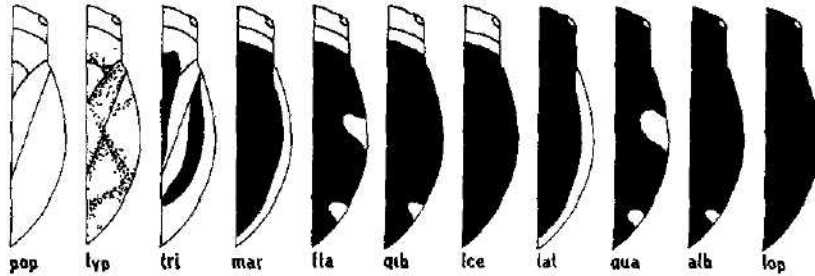


Fig. 1. Colour morphs of *P. spumarius*. Classification according to Halkka et al. (1973).

light morphs, *populi* (pop), *typicus* (typ), *trilineatus* (tri), and dark morphs, *marginellus* (mar), *flavicollis* (fla), *gibbus* (gib), *leucocephalus* (leu), *lateralis* (lat), *quadrimaculatus* (qua), *albomaculatus* (alb), and *leucophthalmus* (lop) (Fig. 1). The transition between some morphs is nearly continuous and the boundaries rather arbitrary. In dubious cases we attributed an individual to less melanized colour form. Sex was determined in 29 populations.

RESULTS

In the total sample of Czechoslovak populations approximately four fifths of animals belonged to light forms. The most abundant form was typ, which formed 36.6—88.4 % in different populations (58.3 % in pooled total sample), and pop (20.1 % of total sample). Tri formed only 4.1 % of the total. The dark forms represented about one fifth of the total sample. The most abundant were lop and qua (4.4 and 3.5 %, resp.), the rarest were gib and lat (0.8 and 0.7 %, resp.). The rare dark forms may appear locally abundant (Tab. 1).

Females had greater tendency to melanism than males. Their prevalence was most conspicuous in lat and mar, where they represented (in pooled sample of sexed populations) 89.3 and 87.9 % of morph total: only in qua, alb, and lop there were ≤ 50 % of females. By contrast, in the lightest form pop the ratio of sexes was reversed and males formed 69.6 % of the morph total. All morphs were represented by both sexes.

The relation was investigated between the melanism in local populations and the environment. The proportion of melanic forms seems to reveal a geographic trend (Fig. 2). The proportion of melanics in the western part of the investigated area was mostly below 25 %. Six populations with >30 % of melanic forms were all captured in the East, in the Carpathian mountains of northern and eastern Slovakia. Here the probability of occurrence of melanic populations increases, although most populations have low percentage of dark forms, too. Melanic populations found by Halkka et al. (1980) were sampled some 30 km easterly from localities 58—62 at Czechoslovak territory.

The proportion of dark forms apparently did not depend on the altitude of sampling site (Fig. 3). Populations with highest proportion of melanic forms were taken

Table 1. Composition of local populations of *P. spumarius* in Czechoslovakia

Locality (Altitude)		pop	typ	tri	mar	fla	gb	lee	lat	qua	alb	lop	Total	% M
1. Horní Blatná (970)	m	25	20	—	—	—	—	—	—	2	3	1	94	10.8
	f	9	28	2	—	1	—	2	1	—	—	—		
2. Boží Dar (1,000)	u	22	48	—	—	2	1	—	1	—	1	3	78	10.3
3. Hvězda (800)	u	17	12	1	—	1	—	—	—	2	3	—	36	18.7
4. Krupá (350)	u	47	84	11	2	9	3	—	1	6	3	3	169	16.0
5. Liběšice (220)	u	62	63	19	3	6	—	—	1	3	6	8	171	15.8
6. Bílina (220)	u	16	31	18	1	1	—	1	—	6	3	12	89	27.0
7. Černčice (500)	m	9	8	1	—	—	—	—	—	2	1	3	65	21.5
	f	10	18	5	—	—	—	—	3	1	1	3		
8. Bouřňák	m	21	21	2	—	1	—	—	—	2	3	—	130	14.6
	f	17	46	4	4	2	1	2	—	1	—	3		
9. Cínovec (870)	m	33	39	1	—	4	—	—	—	8	1	—	163	12.9
	f	23	42	4	—	3	1	—	—	1	3	—		
10. Tolštejn (600)	m	19	47	—	—	2	—	—	—	6	1	1	181	15.5
	f	8	78	1	1	6	—	—	1	8	—	2		
11. Zákupy (280)	u	9	57	6	1	5	—	2	—	1	1	5	87	17.2
12. Lběchov (170)	u	3	21	1	—	4	—	1	1	2	—	1	34	26.5
13. Praha-Ruzyně (380)	m	14	16	3	—	—	—	2	—	3	—	1	87	14.9
	f	8	28	5	—	1	3	2	—	1	—	—		
14. Praha-Ruzyně (360)	m	75	37	12	—	—	1	1	—	13	2	1		
	f	22	87	21	6	7	1	—	—	4	1	2	349	12.6
	u	19	30	3	—	—	—	1	—	1	2	1		
15. Horoméřice (380)	m	22	14	4	—	—	—	—	—	1	1	—	77	6.5
	f	10	18	4	—	2	—	—	—	—	1	—		
16. Krasno (800)	u	—	40	6	—	—	—	1	—	—	—	3	50	8.0
17. Hejnice (380)	u	18	51	2	2	3	—	—	—	2	—	1	79	10.1
18. Bedřichov (760)	u	22	77	7	2	3	1	1	1	14	4	2	134	20.9
19. Antonínov (800)	u	15	83	1	—	1	1	2	2	11	2	8	126	21.4
20. Bílý Potok (500)	u	18	68	2	1	4	2	1	—	5	1	2	104	15.4
21. Pec pod Sněžkou (760)	m	13	17	—	—	—	1	—	—	4	—	2	97	20.6
	f	6	41	—	1	1	—	4	—	5	—	2		
22. Tuklaty (260)	u	15	33	16	1	11	—	—	—	1	2	1	80	20.0
23. Počáňany (230)	u	11	18	4	—	—	—	—	—	3	3	3	42	21.4
24. Čáslav (240)	m	37	73	4	—	—	—	—	—	5	—	—	162	11.8
	f	6	33	3	—	2	—	—	—	5	—	—		
25. Bohdaneč (220)	m	24	18	2	—	—	—	—	—	—	—	1	82	9.8
	f	15	12	3	1	2	1	—	—	—	2	1		
26. Březnice (540)	u	20	25	1	—	—	1	—	—	2	—	—	40	6.1
27. Radomyšl (500)	u	25	32	4	1	5	—	—	—	—	4	2	73	16.4
28. Strakonice (410)	u	32	51	3	1	3	—	3	1	—	2	3	99	13.1
29. Smetanova Lhota (390)	u	18	44	—	—	4	—	3	—	—	6	—	75	17.3
30. Mlýčín (650)	m	41	44	3	—	—	—	—	—	7	2	—		
	f	12	67	3	1	1	—	—	2	13	—	5	250	14.4
	u	10	34	—	—	—	—	1	1	2	1	—		
31. Malotín (680)	u	7	20	1	1	—	—	—	—	—	—	—	29	3.4
32. Frymburk (740)	u	14	15	—	—	1	—	1	—	2	—	2	35	17.1
33. Hrušovany u Brna (180)	u	21	61	5	3	2	1	—	1	2	1	2	99	12.1
34. Tereňov (600)	m	7	10	—	—	—	1	1	1	4	—	6	91	51.6
	f	3	24	—	1	4	—	9	5	1	4	10		
35. Bavančarky (1,200)	m	6	42	1	—	1	—	—	—	1	2	5	122	17.2
	f	7	45	—	—	1	—	4	1	—	1	5		
36. Za Kravarské (1,000)	m	17	50	1	—	1	—	—	1	4	1	4	139	18.7
	f	5	40	—	1	2	1	3	1	3	1	3		
37. Štárovo (130)	u	2	13	3	1	—	—	—	—	—	—	—	19	5.3
38. Chvatiměř (500)	u	3	19	1	—	—	—	2	2	—	—	2	29	20.7
39. Kamenistá dohna (730)	u	1	14	2	3	1	—	1	—	—	—	3	25	32.0
40. Tri Chotáře (1,080)	u	6	15	—	3	2	—	1	—	—	—	2	29	27.6

Locality (Altitude)		pop	typ	tri	mar	fa	gib	lee	lat	qua	alb	lop	Total	%M
41. Tisovec Šarkantca (1,150)	u	4	25	--	--	--	--	--	1	1	--	--	31	6.5
42. Nižná Klaková (1,150)	u	23	140	7	7	8	1	15	--	2	2	17	227	22.9
43. Vrchsúfová (970)	u	23	62	--	--	--	2	3	2	1	--	3	96	11.5
44. Baračka (1,100)	u	5	18	--	--	--	--	--	--	1	--	--	24	4.2
45. Biele Skaly (1,100)	u	14	82	1	--	1	1	2	1	2	3	7	114	14.9
46. Ovčec (1,100)	u	9	37	2	--	1	--	--	--	--	--	--	49	2.0
47. Předné Holsko (800)	u	42	93	9	1	1	--	14	1	4	2	18	185	22.2
48. Jahodná (500)	u	21	43	--	1	1	4	1	--	1	--	--	72	11.1
49. Malatiná (970)	m	2	11	1	--	--	1	--	--	--	1	--	41	29.3
	f	1	14	--	1	2	--	3	--	1	--	3		
50. Velké Borové (1,000)	m	8	29	--	--	--	1	1	--	--	--	7	106	22.4
	f	4	41	--	--	1	2	2	--	2	1	7		
51. Zverovka (1,040)	m	6	27	--	--	--	--	1	--	1	--	2	86	17.0
	f	1	39	--	1	1	--	1	2	2	--	4		
52. Vihorlat (970)	m	1	24	--	--	--	1	4	--	9	2	8	82	47.6
	f	--	18	--	--	1	1	6	--	1	4	2		
53. Velká Trstina (850)	m	--	13	--	--	--	--	2	--	--	--	--	40	22.5
	f	--	18	--	1	2	1	1	2	--	--	--		
54. Strhovské sedlo (685)	m	3	13	--	2	1	2	2	1	--	1	1	40	30.0
	f	3	8	1	1	--	--	1	--	--	--	--		
55. Palota (800)	m	1	6	--	--	--	--	--	--	--	--	4	27	40.7
	f	--	8	1	2	--	--	3	--	1	--	1		
56. Zvala (750)	m	9	31	2	--	1	1	2	--	--	--	8	113	31.0
	f	--	31	5	--	2	1	11	5	2	--	2		
57. Šipková (950)	m	5	47	--	1	--	1	1	--	2	1	9	164	24.4
	f	4	66	2	3	2	1	8	1	1	1	8		
58. Plaša (1,160)	m	2	20	--	--	--	--	--	--	--	--	--	39	10.3
	f	--	13	--	--	--	1	2	--	--	--	1		
59. Ďurkovec (1,190)	m	17	82	--	--	--	--	--	--	--	--	1	188	5.3
	f	5	73	1	1	3	--	2	1	--	--	2		
60. Runina (600)	m	1	29	1	1	--	--	1	--	2	2	6	78	34.6
	f	--	19	1	2	4	--	5	--	--	--	4		
61. Čerňaz (1,070)	m	1	37	1	--	--	2	--	--	--	1	1	89	22.5
	f	--	29	1	1	2	5	6	--	--	1	1		
62. Hrubky (1,180)	m	1	65	--	--	--	--	--	--	2	--	1	146	9.6
	f	2	64	--	--	4	--	4	--	1	--	2		
63. Merboltice (460)	u	20	85	11	1	1	--	5	--	3	--	3	129	10.1
Total	m	414	330	39	4	11	12	18	3	78	25	73		
	f	181	1,048	62	29	59	20	81	25	54	21	73		
	u	617	1,614	152	36	81	17	62	17	79	53	118		
Grand total		1,212	3,522	253	69	151	49	161	45	211	99	264	6,063	
Per cent		20.1	58.3	4.1	1.2	2.5	0.7	2.7	0.7	3.5	1.6	4.4		

m - males, f - females, u - unsexed, M - melanic forms

at altitudes of 600-1,000 m. Some localities with melanic populations might have particular microclimate, e.g. reduced duration of sunshine and temperature inversion in mountain valleys. However, there exist localities with similar geographic characteristics inhabited by populations with low proportion of melanics, e.g. the valleys of Pec pod Sněžkou (21), or Antonínov (19).

No relationship was observed between melanism and industrial pollution (solid smoke outfall, acid rain, or concentration of sulphur dioxide in the atmosphere). North-west Bohemia belongs to the most polluted areas of the world (Hrdá et al..

1977). The pollutants are produced by electric power plants using brown coal, and by heavy chemical industry. In spite of the serious pollution we did not observe any substantial difference between the samples from this region (localities 5–9) with 12.9–27.0 % of dark forms, and samples from typically “rural” areas of southern Bohemia (localities 26–32). Also local effects of pollution by automobile



Fig. 2. The proportion of melanic forms (black sector) in 63 local populations of Czechoslovakia. Numbers of localities are concordant with Tab 1.

exhausts on roadside populations were of little importance. The melanic population of Terchová (34, 51.6 % of melanics) was sampled along the road at Vrátná dolina Valley, with busy traffic. However, other populations of roads with similar automobile traffic, e.g. along the highway at Praha-Ruzyně (13), had low proportion of dark forms. Other melanic populations, e.g. of mountain meadows of Vihorlat (52) or at Palota (55) or from Kamenistá dolina Valley (39), were sampled at non-polluted localities.

DISCUSSION

A great number of works on insect melanism revealed factors which may influence the frequency of morphs. Climatic factors and/or industrial pollution have been often claimed or proved as causes (e.g. Mikkola, 1980, Muggleton, 1978, Popescu, 1979, Schummer, 1976, Steward, 1977). Factors effective at one place may be without importance at another one. A coccinellid, *Adalia bipunctata*, may serve as a paradigm: the relationship between melanism and industrial pollution exists in certain areas (Creed, 1971, 1974, Zakharov and Sergievski, 1978), while in others it does not (Honěk, 1975).

Melanic populations of *P. spumarius* were found in mountain rural areas of Carpathian mountains (Halkka et al., 1980, this work), and in limited areas of urban south Wales, Britain (Lees et al., 1983). The increase of melanics proportion with altitude was explained by linkage of melanic alleles with a supergene selected by high-altitude conditions (Halkka et al., 1980), while for British populations a conspicuous relationship with industrial pollution was demonstrated (Lees and Dent, 1983). Melanic populations thus appear in areas with quite different environmental conditions.

In Czechoslovakia the melanism has obviously little to do with altitude, microclimate, or environmental pollution. There is also little reason for why other mechanisms of selection, predation (Halkka and Mikkola, 1977) or morph-specific impact of parasites (Harper and Whittaker, 1976), should have localized effects. Some melanic populations had rather low density (estimated by the sampling effort,

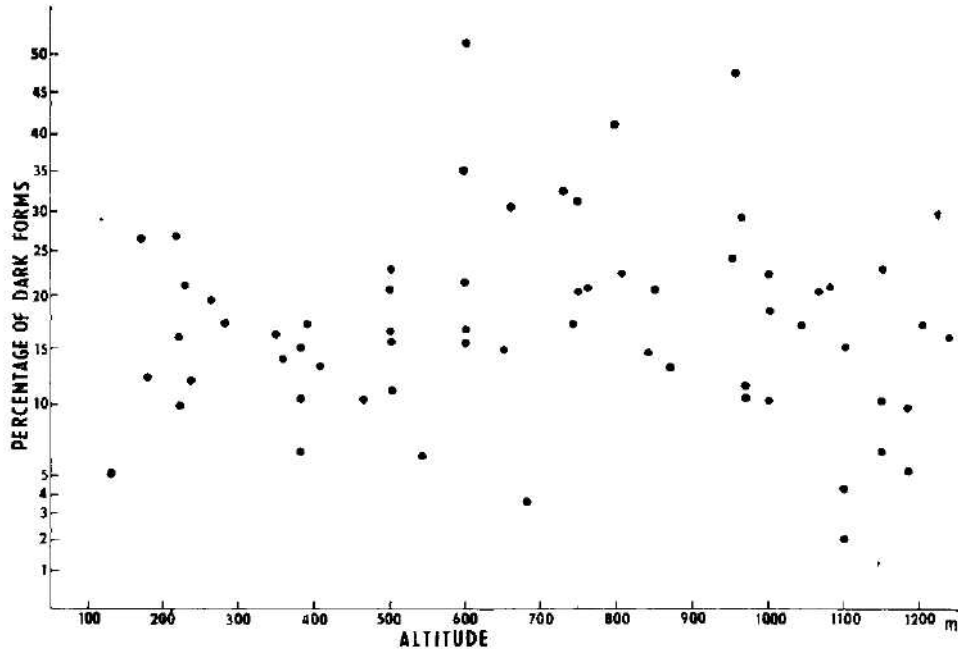


Fig 3. The relation between the altitude of sampling site and the proportion of melanic forms in the population.

i.e. number of sweeps needed to capture an individual). These populations seemed to appear at places with suboptimum conditions. They might develop through morph-specific larval preferences for certain plant species (cf. Halkka and Mikkola, 1977) or through different rates of migration to suboptimum environments. Similar differences between populations of good and bad conditions were observed in case of larval polymorphism in a cicadellid, *Mocycdia crocea* (Müller, 1979).

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**CIRCANNUAL CHANGES IN THE SEXUAL SIZE DIMORPHISM
IN STREPTOPELIA DECAOCTO (AVES: COLUMBIDAE)**

Jiří MLÍKOVSKÝ and Petr ŠVEC

Abstract. Circannual changes in the body weight and sexual size dimorphism in the Collared Dove *Streptopelia decaocto* were studied. Circannual changes in the body weight in both males and females were found to be marked, different from each other and apparently adaptive. On the other hand, circannual changes in the sexual size dimorphism were also found to be marked, but non-adaptive. Factors affecting the phenomena under study are discussed.

INTRODUCTION

Animal species have been traditionally considered either sexually dimorphic or sexually monomorphic in size. It was Selander (1966, 1971, 1972) who showed that this a-priori assumption may not be true, and that the degree of the sexual size dimorphism can considerably vary with respect to different organs within a species. Selander's suggestion has been later corroborated in several studies (e. g. Andersson and Wester 1971, Kushlan 1977, Weatherhead 1980, Johnston and Fleischer 1981, Mlíkovský and Piechocki 1983, in press, Piechocki 1984). In addition, Mlíkovský and Piechocki (1983b), studying the European Common Bussard (*Buteo buteo*) could show that the degree of the sexual size dimorphism can considerably vary circannually.

Their observations will now be tested on the European Collared Dove *Streptopelia decaocto* (Frisvaldszky, 1838). Simultaneously, as only scarce data regarding circannual changes in body weight in the Columbidae (Grundová 1965, Ljunggren 1968, Dvořáková-Grundová 1970, Rana 1975), as well as regarding body weights of the Collared Doves themselves (Kroneisler-Ruchner 1957, Niethammer 1962, Dekker 1963, Grundová 1965, Lachner 1965, Dvořáková-Grundová 1970, Creutz and Piechocki 1970; cf. also Hofstetter and Scherner 1980) have so far been published, the present paper will contribute also to these more specific problems.

MATERIALS AND METHODS

All the Collared Doves studied in this paper (180 males and 165 females) were collected in the Prague Zoological Garden (ZOO Praha) during the year 1976 by Petr Švec and Jan Dřevo. In this area Collared Doves are abundant throughout the year, are non-migratory, and because they mostly feed on corn supplied to various ZOO animals, they always have food ad libitum (Švec 1978).

All birds were killed before weighting and weighted in fresh state by Petr Švec on the "Labora" weight with the accuracy to 0.1 gramm. Crop contents were removed

before weighting. Sex was estimated by dissection after weighting. Age of the collected birds was estimated according to characters given in Lachner (1965) and only adult birds, i. e. birds older than 1 year (age classes II and III of Lachner 1965) were included into the further analysis.

The data obtained were further elaborated by Jiří Mlíkovský. For every month, mean body weight (\bar{x}), its standard error (s_x), standard deviation (s_{n-1}), its standard error (S_s), and coefficient of variation (CV) were calculated for each sex separately using standard formulas of mathematical statistics (see, e. g., Sokal and Rohlf 1969, Weber 1980). Curves in the Figures 3, 4, and 5 were calculated using the method of gliding means (Gebelein 1951). The dimorphism index (D.I.) was calculated as $D.I. = m/f$, where m = mean body weight of males, and f = mean body weight of females, respectively, and tested with the t-test (Sokal and Rohlf 1969).

RESULTS AND DISCUSSION

Circannual changes of the body weight in the Collared Dove are presented in Figures 1 and 2, respectively (see Tables 1 and 2 for exact data). Interestingly enough, their general tendencies in males and females are quite different (cf. Fig. 3), so that the sexual size dimorphism strongly varies during the year in Collared Dove (see Fig. 4 and Tab. 3).

Using these findings, we shall now attempt to discuss both the basic hypotheses concerning the essence and importance of the sexual size dimorphism which are a-priori applicable to doves, namely the ecological and the sexual one.

According to the ecological hypothesis, different sizes of sexes within a species evolved for enabling their niche separation (e. g. Rand 1952, Selander 1966, 1972, Andersson and Norberg 1981). Indeed, this suggestion has been later documented on various vertebrates, especially birds (e. g. Hö-

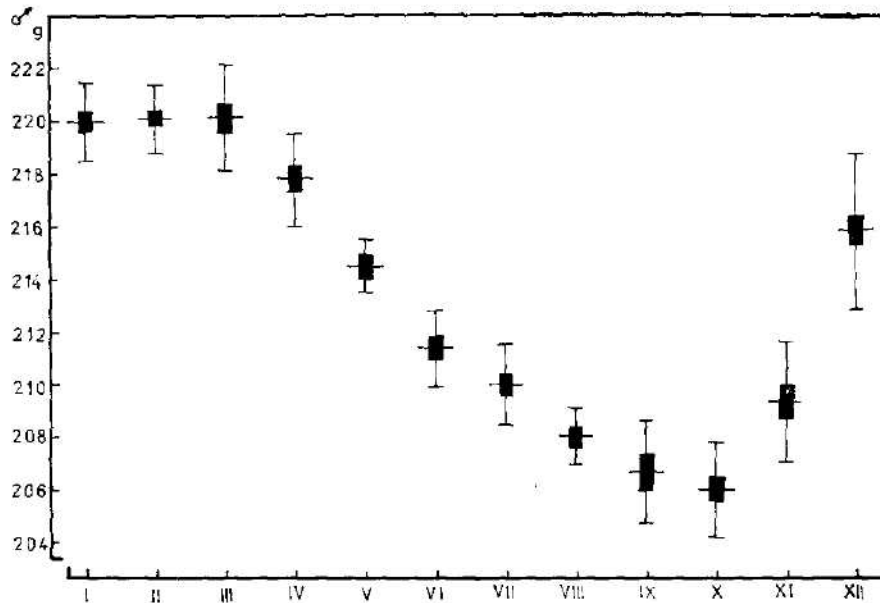


Fig. 1. Circannual changes in body weight of male Collared Doves. Given are mean, its standard error, and standard deviation, Based on data from the Table 1.

glund 1964, Storer 1966, Eahart and Johnson 1970, Brosset 1973, Snyder and Wiley 1976, Mueller et al. 1981).

No such effect is probable in the Collared Dove, although Helešić (1981) detected slight differences between the sexes of this species. He noted, however, that these differences are apparently caused by their different feeding site

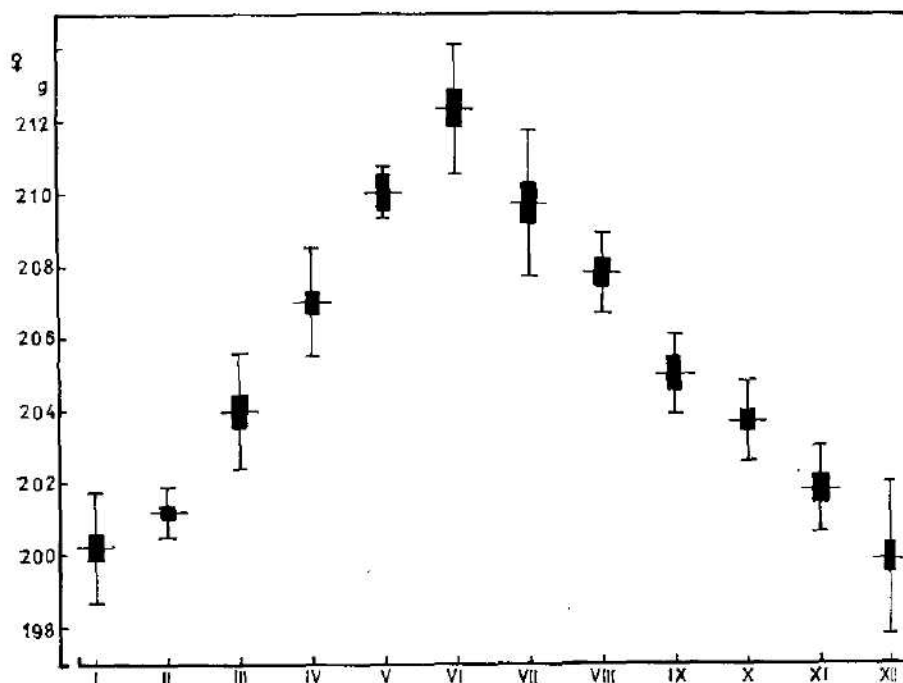


Fig. 2. Circannual changes in body weight of female Collared Doves. Based on data from the Table 2. See Fig. 1 for explanation.

selection. Moreover, he found no correlation between food composition and body size in his study population of the Collared Dove. Although other authors dealing with the study of the food composition of the Collared Dove did not consider sex differences (e. g. Kovacević and Danon 1951, 1957, Fric 1954, Feriancová 1955, Barthos 1957, Tutman 1960, Szlivka 1965, Soviš and Vallo 1966, Bičik and Směšná 1971, 1972, Rekasi 1975, Nowak 1975), we consider Helešić's (1981) results convincing enough to exclude the ecological hypothesis of the sexual size dimorphism in the Collared Dove.

On the other hand, our data seem to agree more closely with the hypothesis which tries to explain sexual size dimorphism in the terms of sexual selection (e. g. Darwin 1871, Nekrasov 1927, Huxley 1938, Kistjakovskij 1958, Amadon 1959, Davitašvili 1961, Mayr 1972, Trivers 1972, Searcy 1982, and many others). However, as we shall explain further below, we believe that the sexual size dimorphism is not selected for in the Collared

Table 1. Body weight statistics in male Collared Doves.
Weights in gramm. CV in %

month	\bar{x}	s_x	s_{n-1}	s_x^+	CV	scv	n
I	219.91	0.327	1.427 ⁺	0.231	0.649	0.105	19
II	221.14	0.270	1.210	0.191	0.547	0.086	20
III	221.39	0.528	1.974	0.373	0.892	0.169	14
IV	217.83	0.507	1.829	0.359	0.840	0.165	13
V	214.52	0.439	0.983	—	0.458	0.145	5
VI	211.42	0.399	1.437	0.282	0.650	0.133	13
VII	209.71	0.395	1.528	0.279	0.729	0.133	15
VIII	208.45	0.379	1.073	—	0.515	0.129	8
IX	206.66	0.676	1.912	—	0.925	0.231	8
X	206.26	0.419	1.778	0.296	0.862	0.144	18
XI	209.23	0.594	2.300	0.420	1.099	0.201	15
XII	215.83	0.516	2.918	0.365	1.352	0.169	32
I—XII	214.32	0.425	5.708	0.301	2.663	0.140	180

⁺) Not calculated for too small samples.

Dove, i. e. that it is non-adaptive (but not maladaptive!) (cf. Gould and Lewontin 1979, and Hilborn and Stearns 1982 for recent critics of the adaptationists program). On the contrary, we are convinced in the adaptiveness of circannual body size changes within both sexes of the Collared Dove separately.

Let us take males at first. Their body weight falls to its minimum in October, then rises fastly up to its maximum which it reaches in January through March. Since April their body weight falls again slowly to its minimum in October (see Fig. 1). Now, we have to search for the reasons for the location of these

Table 2. Body weight statistics in female Collared Doves.
Weights in gramm. CV in %

month	\bar{x}	s_x	s_{n-1}	s_x^+	CV	scv	n
I	200.25	0.330	1.512	0.233	0.755	0.117	21
II	201.18	0.172	0.686	0.121	0.341	0.060	16
III	203.98	0.445	1.603	0.314	0.786	0.154	13
IV	207.00	0.444	1.471	0.314	0.711	0.152	11
V	210.02	0.288	0.765	—	0.336	0.097	6
VI	212.29	0.508	1.760	0.359	0.829	0.169	12
VII	209.69	0.547	1.973	0.387	0.941	0.184	13
VIII	207.80	0.410	1.085	—	0.521	0.140	7
IX	205.02	0.459	1.123	—	0.548	0.158	6
X	203.69	0.244	1.120	0.173	0.550	0.085	21
XI	201.83	0.362	1.201	0.256	0.595	0.127	11
XII	199.88	0.396	2.094	0.280	1.047	0.140	28
I—XII	204.03	0.340	4.364	0.240	2.139	0.118	165

⁺) Not calculated for too small samples.

cardinal points. There are, we believe, three a-priori reasonable explanations for high body weights of the male Collared Doves in winter months, as follows:

(1) Large body size provides advantage during severe winter weather. — Although the mortality of Collared Doves seems to be largest in winter (cf. Rost

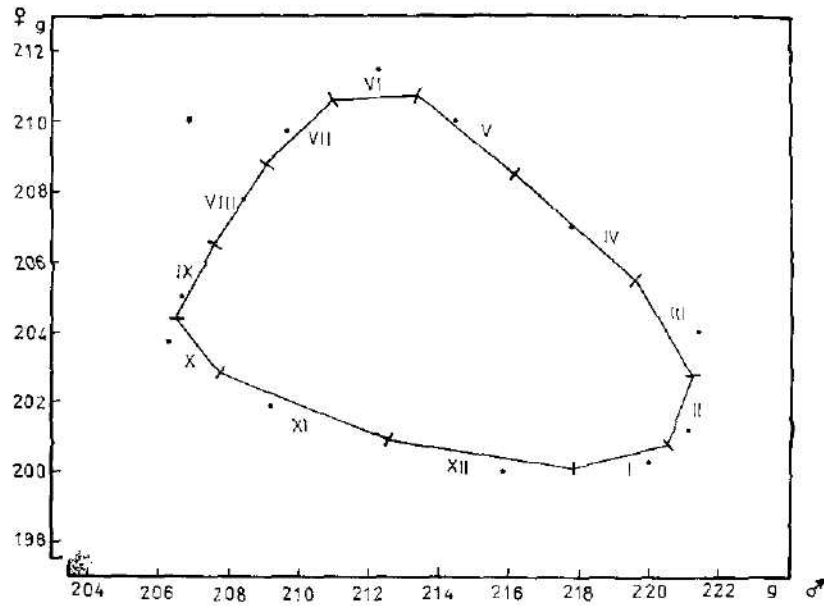


Fig. 3. Circannual changes in the relation between absolute body weights of male and female Collared Doves. Based on the data from the Tables 1 and 2.

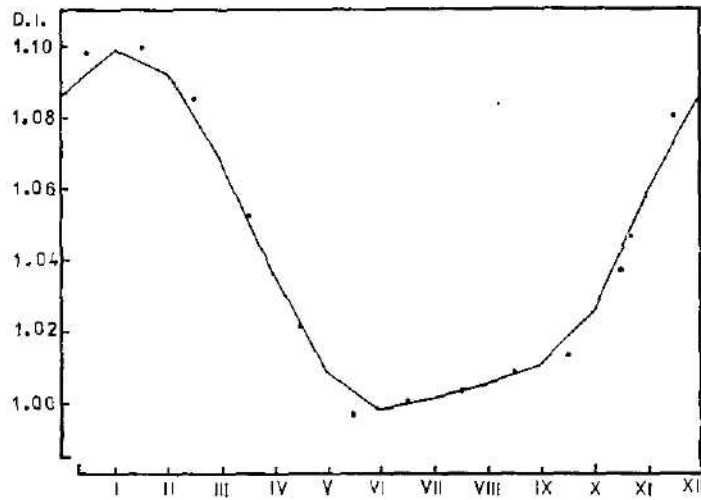


Fig. 4. Circannual changes in the sexual size dimorphism in the Collared Dove. Based on data from the Table 3.

Table 3. Circannual changes in the sexual size dimorphism in Collared Dove.
 Calculated from data given in Tables 1 and 2.
 Significance: ++ = $p < 0.01$, + = $p < 0.1$, — = $p > 0.1$

month	D. I.	Sign.
I	1.098	++
II	1.099	++
III	1.085	++
IV	1.052	++
V	1.021	++
VI	0.996	—
VII	1.000	—
VIII	1.003	—
IX	1.008	—
X	1.013	++
XI	1.037	++
XII	1.080	++
I—XII	1.050	++

1957, Dyrce 1961, Nowak 1965, 1976, Gnielka 1975), larger individuals are in general less vulnerable to cold (cf. Pomarnacki 1960), and larger individuals of the Collared Dove had usually more food in crop than smaller ones (Helešic 1981). This may enable them to survive long cold winter nights better, because they begin to roost at evening with full crops and digest their content till next morning (Murton et al. 1964, Bičík and Směšná 1971, Helešic 1981). Despite of this we consider this explanation improbable, because female Collared Doves reach during winter months their body weight minimum, and all of the above mentioned selection factors should work similarly on both males and females, the more that they build large common flocks during winter (cf., e. g., Feriancová 1955, Lachner 1963, Nowak 1965, Bičík and Směšná 1971, Hudson 1972, Reichholf 1976, Švec 1978, Helešic 1981).

(2) Large body size is advantageous in intrasexual selection. — The Collared Dove is monogamous, territorial species in which males are responsible for the gain and maintenance of the breeding territory (cf., e. g., Bodenstern 1949, Hofstetter 1954, Tomasz 1955, Nowak 1965). Hence, larger males probably have more success in gaining a territory (or a better territory) than smaller ones. Because the area for breeding is apparently limited in ZOO Praha, and because there is, consequently, a relatively large floating population of Collared Doves there (see Švec 1978), it is probable that a (how strong?) intrasexual selection between males occurs, in which larger males may be more advantageous. Because the time of mating coincides well with the maximum body size in studied Collared Dove males, we believe that the hypothesis under discussion may be one of explanations for their high body weights during January through March. This is indirectly supported also by Grundová (1965, Dvořáková-Grundová 1970) who found a correlation between the body size increase and the increase in gonadal activity in male Collared Doves. This is not surprising because both the increase of gonadal

activity (Murton and Westwood 1977) and body weight changes (Palya et al. 1983) are controlled by light cycle in columbids.

(3) Larger males are preferred by females during the intersexual selection. – It has been proved experimentally that columbid females select their mates according to their individual, personal characteristics (Morris and Erickson

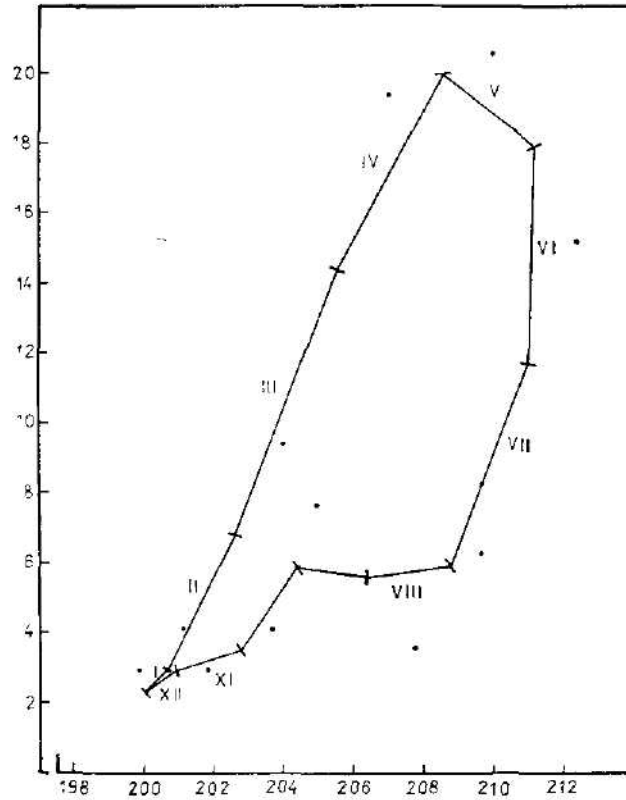


Fig. 5. Circannual changes in the relation between the frequency of breeding and absolute weights of female Collared Doves. Based on data from the Tables 3 and 4

1971, Burley 1977, 1981, Burley and Moran 1979). Although we dispose of no empirical data regarding whether body size belongs to the characters selected for by Collared Dove females or not, it is probable that intersexual selection accounts for the large body size in male Collared Doves during winter months, too.

Let us now turn to the question why a decrease of body weight occurs during spring and summer months in male Collared Doves. Because food is always available ad libitum for Collared Doves in ZOO Praha (Švec 1978), food shortage cannot account for these low weights. Another possible explanation could be molt, because it is energetically rather expensive for most birds (cf. Payne 1972, Dol'nik 1975, Murton and Westwood 1977), but

Table 4. Breeding season of the Collared Dove in ZOO Praha.
From Švec (1978)

month	n	%
I	3	2.50
II	5	4.17
III	15	12.50
IV	28	23.33
V	25	20.83
VI	15	12.50
VII	8	6.67
VIII	3	2.50
IX	8	6.67
X	5	4.17
XI	2	1.67
XII	3	2.50
I—XII	120	100.01

Columbidae are exceptional in this respect. As documented by Murton and Westwood (1977), production of milk by which columbids feed their young reduced their need for energy peaks (see also Brisbin 1969), and enabled them, consequently, to breed and molt partly simultaneously (see, e. g., Murton and Westwood 1977, and Švec 1978). Hence, the energy requirements for molt seem not to cause the decline of body weight observed during summer and fall in male Collared Doves. Due to the absence of other reasonable hypotheses, we are, then, forced to leave this problem open.

Let us now to discuss reasons for the seasonal changes in body weight in female Collared Doves. Their body weight cycle reaches its peak in June, i. e. in the time when the weight of males already heavily declines. For this reason we see no way how this peak could be correlated with any climatic factor. Because the time when female Collared Doves reach their body weight maximum coincides with their preferred breeding season (cf. data in Švec 1978 and our Fig. 5), it seems highly probable that the reasons for this mode of seasonal body size changes are to be searched for in the reproduction (*sensu lato*). Briefly summarized, larger females have in comparison with smaller ones the following respective advantages:

(1) They are able to breed earlier in the year. — This has been well documented for various bird species (e. g. Murton and Isaacson 1962, Murton et al. 1963 a, b, Ryder 1970; cf. also Gates and Woehler 1968, Milne 1976 and Woodall 1981). This can be indirectly supported by our data (Fig. 5), too, which show a clear linear positive correlation between the increasing frequency of breeding and the increasing mean body weight of female Collared Doves in ZOO Praha. Early breeding is advantageous because early fledged young have better chance for subsequent survival, as has been evidenced in *Columba* spp. (Murton 1961, 1966), as well as in several non-columbid bird species (Perrins 1963, 1966, Kluijver 1971, and others).

(2) They lay larger eggs. — This has been evidenced, e. g., by Väisänen 1969, Väisänen et al. 1972, Murton et al. 1974, Lundberg and Väi-

säinen 1979 and Mills 1979. The advantage of this consists in the positive correlation between the survival of young and the size of eggs from which they hatched (cf., e. g., Parsons 1970, 1972, 1975, Nisbet 1973, 1978, Schifferli 1973, Davis 1975, Lundberg and Väisänen 1979, Schreiber et al. 1979, Boersma et al. 1980, Ankney 1980, Coulter 1980, Mänd 1980, 1983, Moss et al. 1981, Moss and Watson 1982).

We believe that these selective advantages are convincing enough to explain why female Collared Doves reach their maximum body weight during the peak of their breeding season. However, similarly as in males, we are not able to find any reasonable explanation for the marked weight decrease after the breeding season, especially in winter (cf. the discussion of this problem in the section on males), and leave, hence, the latter problem open in females, too.

CONCLUSIONS

Seasonal changes in the body weight and sexual size dimorphism were studied in the Collared Dove (*Streptopelia decaocto*) population inhabiting Prague Zoological Garden. It is concluded that:

- (1) Changes in the sexual size dimorphism are marked, but not adaptive.
- (2) Changes of the body weight of each sex separately are adaptive, though possible explanations were found for maximum weights only, not for minimum ones.
- (3) Maximum body weight of males coincides with the time they compete for territories (intrasexual selection), and large size belongs, perhaps, to characters preferred by females during their mate selection (intersexual selection).
- (4) Maximum body weight of females coincides with their main breeding season. This is probably because (a) larger females breed earlier and earlier fledged young have better probability to survive, and (b) larger females lay larger eggs and young hatched from larger eggs survive better.

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**OCCURRENCE OF ENDOPARASITIC HELMINTHS IN CARP (CYPRINUS CARPIO)
FROM THE MÁCHA LAKE FISHPOND SYSTEM**

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Dedicated to Prof. Dr. S. Hrabě, DSc. on occasion of his 85th birthday

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Abstract: A survey of the endoparasitic helminths (5 species of Trematoda, 5 Cestoda, 4 Nematoda, 2 Acanthocephala) found in 124 specimens of carp (*Cyprinus carpio* L.) from the Mácha Lake fishpond system (R. Elbe basin, N. Bohemia) in Czechoslovakia is presented. In addition to data concerning the prevalence and intensity of infection and the occurrence of these helminths in other fishes of this locality, for some parasites the seasonal changes in the rate of infection, maturation, and the preference to the various size groups of this host are also described. These questions are discussed in relation to the helminth life cycles and ecological conditions in the locality.

The fishpond system of Mácha Lake, consisting of two large ponds (Mácha Lake — 350 ha and fishpond Břehyně — 270 ha) near Doksy in North Bohemia, Czechoslovakia, connected with one another by some 2 km long "canal" (the Břehyně Brook), represents a very useful locality for studies on the biology and ecology of fish helminths; its characterization has been given in the author's earlier paper (Moravec, 1979a). Investigations into the fish parasites of this locality were started as early as in the 1960's and the data obtained are dealt with in several publications (Moravec, 1978a, b, c, 1979a, b, 1983, 1984a, Moravec and Dyková, 1978). Following the evaluation of the helminthofauna of pike (Moravec, 1979a), this paper presents the results of observations on the endohelminth occurrence in the population of carp (*C. carpio* L.), economically the most important species of freshwater fish in Czechoslovakia and elsewhere; it is part of a broader investigation into the ecology of host — parasite relationships in fish populations of this locality.

MATERIALS

Most fishes were collected using the electric fishing machine in the canal interconnecting both the fishponds (Mácha Lake and fishpond Břehyně), only several fish specimens were obtained when the fishpond Břehyně was emptied in November 1981. The occurrence of endohelminths was traced in carp (*Cyprinus carpio* L.), length 13—40 cm (age 0+—2+), whose regular monthly samples were taken from March 1981 until October 1982. In some months only less than 10 specimens were obtained and, therefore, this material was supplemented with that recovered from carp in various seasons in 1966 and 1975—77. In addition to 124 specimens of carp, also 195 tench, *Tinca tinca* (L.), 79 bream, *Abramis brama* (L.), 67 roach, *Rutilus rutilus* (L.), 67 rudd, *Scardinius erythrophthalmus* (L.), 1 sunbleak, *Leucaspis delineatus* (Heck.), 1 chub, *Leuciscus cephalus* (L.), 16 gudgeon, *Gobio gobio* (L.), 4 crucian carp, *Carassius carassius* (L.), 271 pike, *Esox lucius* L., 2 pikeperch, *Stizostedion lucioperca* (L.), 339 perch, *Perca fluviatilis* L., 6 ruffe, *Gymnocephalus cernuus* (L.) and 132 eel, *Anguilla anguilla* (L.) were examined from this locality. While examining carp, attention was paid to endohelminths only, but oc-

asionally also some ectoparasites were recorded on them: *Dactylogyrus extensus* Mueller et Van Cleave, 1932, *Gyrodactylus katharineri* Malberg, 1964, *Piscicola geometra* (Linnaeus, 1761) *Ergasilus sieboldi* Nordmann, 1832, *Argulus foliaceus* (Linnaeus, 1758) and *Anodonta cygnaea*, glochidia.

SURVEY OF ENDOPARASITIC HELMINTHS OF CARP

1. *Sanguinicola inermis* Plehn, 1905

Adult trematodes of this species were recorded only from the heart of carp; the overall prevalence was 15 %, intensity of infection 1–4 trematodes per fish. Table 1 indicates that there are distinct differences among the recorded values of prevalence of individual monthly samples; the trematodes appear to be present in the heart of carp most frequently in the cool winter and spring months, whereas a substantial decrease in their numbers occurs in a warm period from June until October (in June and August–October they were not found at all). It seems to be in accordance with data by Lucký (1964) who has shown that in the spring and early summer the trematodes occurred mostly (80 %) in the heart and ascending aorta of carp and only in 20 % in their gill arteries, while in July and August, the time of egg release of *S. inermis*, 95 % of the trematodes were in the gill arteries. Scheuring (1923), Naumova (1961), Řehulka and Tesarčík (1971) and other authors observed that the egg development of this blood parasite was temperature dependent with optimum water temperatures for this development occurring in summer; a drop of temperatures resulted in its slowing down.

In the locality in question *S. inermis* was recorded only from *C. carpio*; this confirms a high degree of host specificity of this parasite, experimentally demonstrated by Naumova (1961). According to Scheuring (1923) and some other authors *S. inermis* is mostly found in young carp, while Ivasik (1957) reported increased infections with fish age. Our observations (Fig. 1A) do not indicate a clear dependence of the prevalence and intensity of *S. inermis* infection values on the size (age) of host fishes and the fluctuation found in them is probably associated with the seasonal periodicity in shedding of cercariae from the snail intermediate hosts. The source of infection for fishes are the cercariae, penetrating actively through the skin or gills into the host's blood system. Although body surface is smaller in young fish than in older ones, the effect of this factor is in this case apparently balanced by the fact that their skin tissues are softer and more permeable for the cercariae than in older fish. It probably results in a balanced rate of *S. inermis* infection in younger and older carp.

Sanguinicola inermis is a well-known causative agent of a serious disease in pond-reared carp, leading sometimes, particularly in young fish, to their mortalities. The intermediate hosts of this pathogenic parasite are various species of freshwater snails of the family Lymnaeidae (*Lymnaea auricularia*, *L. stagnalis*, *L. peregra ovata* and others).

2. *Allocreadium carparum* Odening, 1959

Ergens (1964) considered this species a synonym of *A. isoporum dubium* Koval, 1957 but recent studies of the present author (Moravec, 1984b) have indicated *A. carparum* to be a valid species, distinctly different in its morphology from *A. isoporum*. *A. carparum* seems to be a specific parasite of carp, this being also confirmed by our studies carried out in the Mácha Lake fishpond system.

In this locality *A. carparum* is one of the most frequent parasites of carp and it was recorded from 44 % of the examined carp with the intensity 1—480 (average 33) parasites per fish; the trematodes were localized along the whole length of the intestine, but largely in its anterior (juvenile forms) and middle sections. The prevalence ranged from 27 to 75 % in the months when no less than 10 fishes were exam-

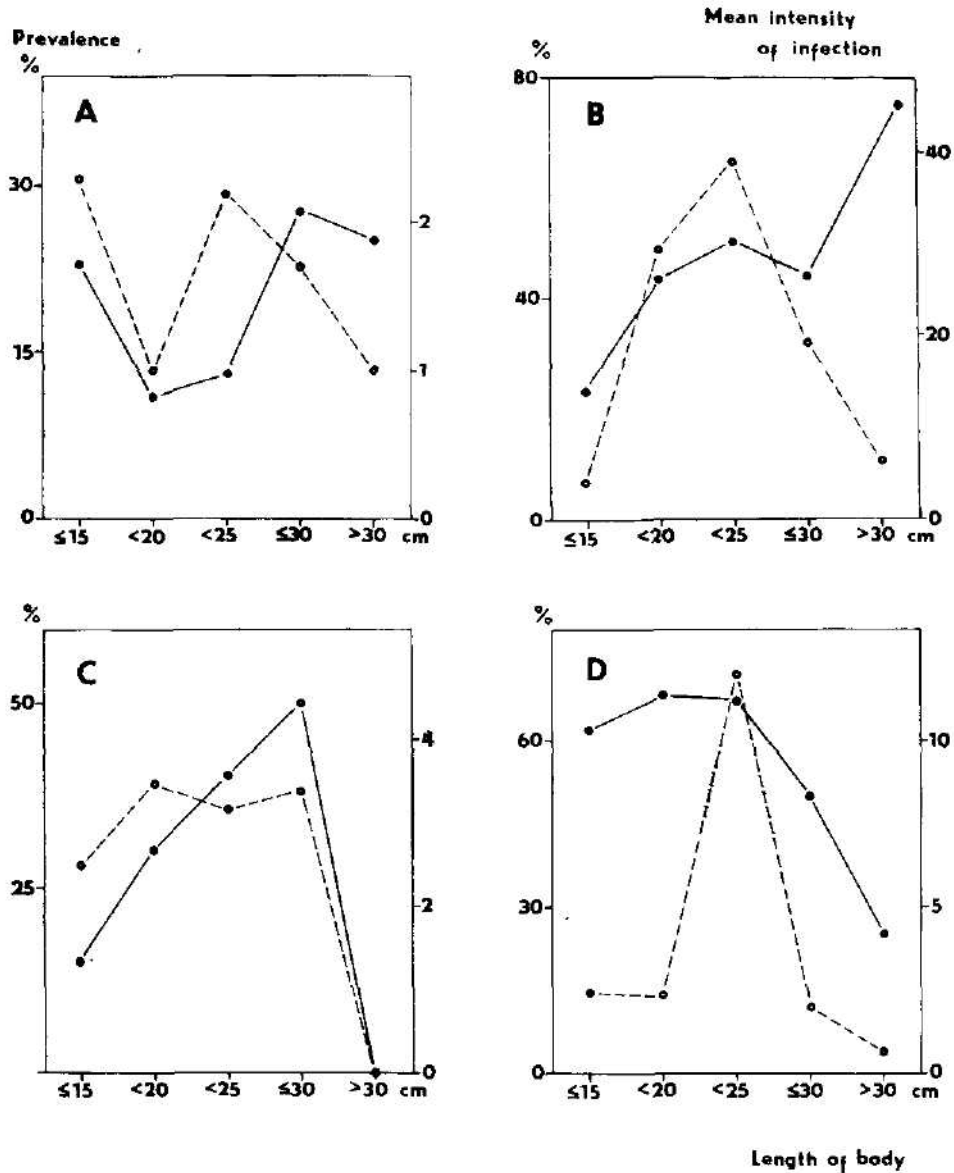


Fig. 1. Relationship of prevalence (—) and mean intensity of infection (-----) to body length of carp: A — *Sanguinicola inermis*, B — *Allocreadium carparum*, C — *Diplostomum spathuceum*, D — *Pseudocapillaria brevispicula*.

ined (Table 1). The distribution of trematodes was uneven within the carp population, being influenced considerably by the body size of host fishes. Fig. 1B indicates that the values of prevalence increase with the host's body length to reach their maximum in the group of the largest carp (body length above 30 cm), while the mean intensity first increases with fish size, attaining its maximum in carp 20–25 cm long, and then again decreases. This is apparently correlated with differences in the composition and amount of food among individual size groups of carp: with gradually increasing volume of taken food, also the probability of in-

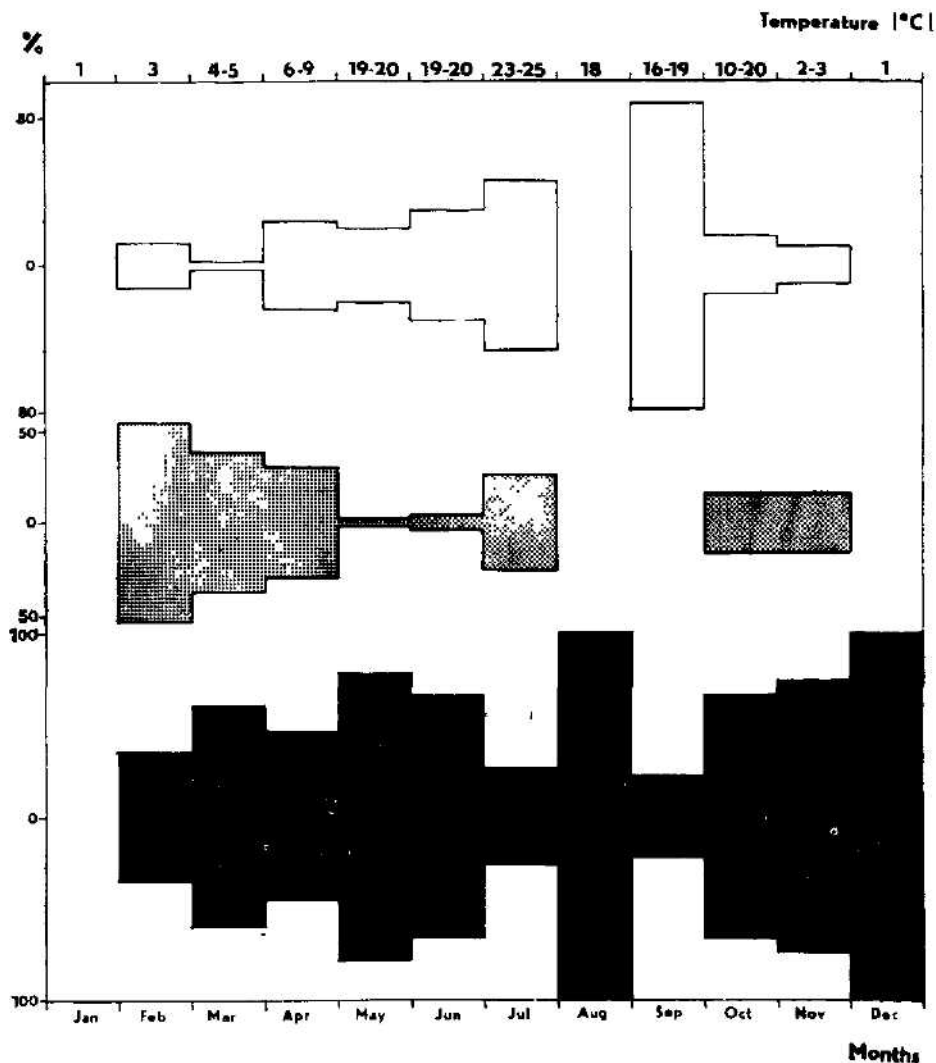


Fig. 2. Monthly changes in occurrence and state of maturity of *A. carparum* in carp of the Mácha Lake pond system (data combined from 1981 and 1982). The data are expressed as percentages of the total number of trematodes found per month: juvenile specimens without eggs, body length below 1 mm (unshaded), young specimens without eggs, body length 1–2 mm (stippled), and mature specimens containing eggs, body length 2–3.5 mm (black).

gesting the intermediate hosts of *A. carparum* (probably clams or larvae of aquatic insects) increases, resulting in the gradual increase of prevalence and in smaller carp also of mean intensity of infection; however, the proportion of the intermediate hosts of *A. carparum* probably decreases in the food of larger carp, this being associated with their food choice. It suggests that the main source of infection for carp are some small-sized intermediate hosts, perhaps members of *Pisidium*. But neither within fishes of the same size group the distribution of *A. carparum* is even and it exhibits a high degree of overdispersion.

It is obvious from Table 1 that this parasite is present in carp all the year round (it was not found only in January when a single fish was examined); even though only less than ten fish specimens were examined in some months and, accordingly, the data from these months are not reliable, the infestation of carp seems to be somewhat lower in a warm period from June till October, which is shown mainly by the values of intensity of infection. Fig. 2 shows that *A. carparum* does not exhibit a clear-cut seasonal cycle in maturation in this locality, but adult trematodes containing eggs are present in carp during the whole year (not recorded only in January when a single fish was examined). Also juvenile trematodes were present in fishes in all months except for January and August; it suggests that new infections are acquired by fish nearly throughout the year, but mostly during a warmer period from April to November. The absence or presence of only a small number of juvenile trematodes in winter months (December—March) may be connected with the fact that carp do not feed or take only a small amount of food in this season by which acquiring new *A. carparum* infections is either made impossible or considerably decreased. The presence of only gravid trematodes in August may be associated with a rapid maturation of the trematodes obtained in spring due to increased water temperature and absence of new infections in August, and perhaps also with the host's choice of food and other factors.

The seasonal occurrence and maturation of *A. carparum* have not been studied so far. In *A. isoporum*, a closely related species parasitizing various cyprinids, Davis (1967) and Koval (1952) found distinct seasonal cycles in maturation and occurrence of these trematodes in the river fish populations in England and the Ukraine, respectively; however, Kozička (1959) at lakes in Poland was unable to observe a distinct periodicity of *A. isoporum*, which was very common in summer and autumn months; Malakhova (1961) reported this species from *Rutilus rutilus* during all seasons in Lake Konche in Karelia, USSR.

The intermediate hosts of *A. carparum* are not known; since this trematode is an important parasite of pond-reared carp, a recognition of its life cycle would be desirable. As the first intermediate host of the related species *A. isoporum* serves the clam *Sphaerium rivicola* in which oculate cercariae develop; encysted metacercariae are also found in *Sphaerium* (in the same or different individuals) (Dollfus, 1949, Wisniewski, 1958, Yamaguti, 1975). In other related species, *A. papilligerum*, the first intermediate host is *Pisidium casertanum*, while ephemeropteran larvae of the genera *Caenis* and *Baetis* serve as the second one (harbouring metacercariae) (Lambert, 1974, Moravec, 1984b). Members of both *Sphaerium* and *Pisidium* are abundant in the Mácha Lake fishpond system (Flasar, 1964); these molluscs constitute here a significant food component of carp (Table 2).

3. *Phyllodistomum elongatum* Nybelin, 1926 juv. (Fig. 4E, F)

Juvenile specimens of this species were found in only four young carp (body length 14—20 cm), prevalence 3.2 %, intensity 1—22 (average 8) parasites per fish.

examined in the summer (July, August); they were localized in the urinary system (urinary bladder, ureters, kidneys), only the smallest specimen was found in the gut. The body of these trematodes was 0.54–1.12 mm long and 0.299–0.313 mm wide, the size of oral sucker 0.105–0.135 × 0.111–0.144 mm, of acetabulum 0.135 to 0.168 × 0.138–0.180 mm; size ratio of suckers was 1 : 1.22–1.37; vitellaria still indistinct; eggs lacking.

Adult *Ph. elongatum* containing eggs were recovered in this locality only from *Tinca tinca*, the latter being here apparently the main host of this parasite (prevalence 5 %, intensity 1–30); besides *C. carpio*, juvenile trematodes were found as well in *Scardinius erythrophthalmus* (prevalence 4.4 %, intensity 1–3). It has not been determined whether the trematodes may attain maturity and produce eggs in the latter two hosts (*C. carpio* and *S. erythrophthalmus*); however, in the literature both these fish species are reported to be the hosts of *Ph. elongatum* (see Pigulevskiy, 1953).

According to Orecchia et al. (1975) the development of *Ph. elongatum* involves one mollusc intermediate host, *Anodonta cygnea*, in which large-tailed rhopalocercous cercariae develop. The metacercariae, encysted inside their transformed tails and floating in water, are the main source of infection for fishes. I found the fully developed cercariae of *Ph. elongatum* in 1 of the 5 *Anodonta cygnea* examined occasionally from the Mácha Lake pond system in April 1982. The body of these cercariae (without tail) was approximately of the same size as that of juvenile trematodes from carp.

4. *Diplostomum spathaceum* (Rudolphi, 1819) — metacercariae

The metacercariae of *D. spathaceum* localized in the lens of the eye are relatively frequent parasites of carp in this locality; no substantial changes in the infestation of carp during the year are obvious from the comparison of individual monthly samples. The overall prevalence in *C. carpio* was 33 %, but intensity only 1–19 (average 4) specimens per fish. The prevalence ranged from 23 to 30 % in the monthly samples when at least 10 fishes were examined; the values from January and February (100 % and 0 %), differing markedly from the overall prevalence, were evidently influenced by small numbers of examined fishes.

However, there are distinct differences in the infestation of the individual size groups of carp; Fig. 1C indicates a linear increase in prevalence with the size of fish attaining its peak in carp 25–30 cm long; also the mean intensity first slightly rises but latter keeping more or less the same level; however, both these values fall suddenly in the group of the largest carp. This decline may be connected with a more pronounced resistance of the largest fish against new invasions and with a limited length of life of metacercariae; according to Shigin (1964) the life span of metacercariae in their principal host, *Rutilus rutilus*, was about 3–4 years, but much shorter in other species of fishes, depending on the degree of adaptation of the parasite to the particular species of fish. A considerable drop in prevalence in oldest fish was also observed by Titova (1957) in *Abramis brama* from Lake Ubinsk in Siberia.

In addition to carp, many other fish species, mainly cyprinids, were parasitized by this pathogenic helminth in the locality investigated: *Abramis brama* (prevalence 90.1 %, intensity 5–120), *Rutilus rutilus* (prevalence 59.7 %, intensity 1–210), *Leuciscus cephalus* (1 specimen found in 1 fish examined), *Gobio gobio* (prevalence 87.5 %, intensity 2–30), *Leucaspis delineatus* (1 specimen found in 1 fish examined), *Carassius carassius* (prevalence 25 %, intensity 1), *Scardinius erythrophthalmus*

(prevalence 1.5 %, intensity 1), *Tinca tinca* (prevalence 5.3 %, intensity 1–3), *Esox lucius* (prevalence 1.4 %, intensity 1–12) and *Gymnocephalus cernuus* (prevalence 50 %, intensity 1–5).

As first intermediate hosts of *D. spathaceum* are reported snails of the genus *Lymnaea*, the principal definitive hosts in Czechoslovakia are gulls (*Larus ridibundus*) (see Vojtek, 1974).

5. *Cotylurus pileatus* (Rudolphi, 1802) — metacercariae

Metacercariae of this species were recovered in the only carp (body length 15 cm) examined in April 1981 (prevalence 0.8 %); five whitish, oval-shaped cysts containing these metacercariae were localized on the gut-surface. The development of this species is not sufficiently known. The encysted metacercariae are reported from a number of fish species (mainly cyprinids), the definitive hosts being the fish-eating birds of the family Laridae, in Czechoslovakia *L. ridibundus* (see Vojtek, 1974).

Cestoda

6. *Caryophyllaeus fimbriiceps* Annenkova-Chlopina, 1919

A young specimen (length 12 mm) of this species, still without eggs, was found in the intestine of a single carp (body length 19 cm) in June 1982 (prevalence 0.8 %). As intermediate hosts of this species serve the oligochaetes *Tubifex tubifex* according to Bykhovskaya-Pavlovskaya et al. (1962).

7. *Proteocephalus percae* (Müller, 1780) juv.

Very young specimens of this cestode (body length 1.4–2.9 mm) were found in the middle and posterior sections of intestine in two carp (body length 24 and 27 cm) examined in November 1982 (prevalence 1.6 %, intensity 1–2). Since *P. percae* is the only representative of the genus occurring in this locality, the juvenile specimens were assigned to this species. The definitive hosts are here *Perca fluviatilis* (prevalence 33 %, intensity 1–40) and *Gymnocephalus cernuus* (prevalence 16 %, intensity 15). Undoubtedly, carp is only a transitive host acquiring invasions while feeding occasionally on small infected perch; the cestodes can apparently survive in the gut of this host for some time without any development. The intermediate hosts of *P. percae* are various species of copepods.

8. *Triaenophorus nodulosus* (Pallas, 1791) — plerocercoid

A live plerocercoid of this cestode (body length 6.5 mm) was found in the anterior part of intestine of one carp (length 27 cm) examined in July 1982 (prevalence 0.8 %). This is an incidental finding, when carp acquired the plerocercoid by swallowing up infected perch; the latter fish serves as the second intermediate host of *T. nodulosus* in this locality; apparently, after digestion of perch the plerocercoid is shortly passaged through the carp's intestine. *T. nodulosus* plerocercoids were recovered only from *Perca fluviatilis* (prevalence 31 %, intensity 1–35) in this locality, the definitive host of this cestode being here *Esox lucius* (prevalence 55 %, intensity 1–54). The development of *T. nodulosus* involves two intermediate hosts: the first one are various copepods, the second one some fishes (largely perch).

9. *Valipora campylancristota* (Wedl, 1855) — plerocercus (Fig. 4G, H)

A single larva of this cestode was found in the gall-bladder of one young carp (body length 14 cm) (prevalence 0.8 %) examined in August 1976; it was not re-

Table 1. Survey of *Cyprinus carpio* examined from the Macha Lake pond system in 1981—82 and their infection by *Sanguinicola inermis*, *Allocreadium carparum*, *Diplostomum spathaceum* and *Acanthocephalus lucii*.

Month	<i>Sanguinicola inermis</i>			<i>Allocreadium carparum</i>			<i>Diplostomum spathaceum</i>			<i>Acanthocephalus lucii</i>			Body length of carp in cm (mean, range)
	No. of carp examined	No. of carp infected (Prevalence)	Intensity (mean, range)	No. of carp infected (Prevalence)	Intensity (mean, range)	No. of carp infected (Prevalence)	Intensity (mean, range)	No. of carp infected (Prevalence)	Intensity (mean, range)	No. of carp infected (Prevalence)	Intensity (mean, range)		
January	1	0 (0%)	—	0 (0%)	—	1 (100%)	4 (4)	0 (0%)	—	0 (0%)	—	18 (18)	
February	4	1 (25%)	3 (3)	3 (75%)	262 (13—480)	0 (0%)	—	1 (25%)	1 (1)	1 (25%)	—	21 (19—22)	
March	6	2 (33%)	2 (1—2)	3 (50%)	21 (15—26)	4 (67%)	6 (1—19)	0 (0%)	—	0 (0%)	—	24 (21—28)	
April	13	3 (23%)	1 (1—2)	8 (62%)	35 (6—92)	3 (23%)	1 (1—2)	0 (0%)	—	0 (0%)	—	17 (15—26)	
May	17	5 (29%)	2 (1—3)	6 (35%)	44 (1—131)	5 (29%)	3 (1—10)	1 (6%)	2 (2)	1 (6%)	—	17 (13—26)	
June	20	0 (0%)	—	7 (35%)	7 (2—16)	6 (30%)	9 (2—11)	5 (25%)	1 (1)	5 (25%)	—	17 (14—26)	
July	10	2 (20%)	1 (1)	4 (40%)	5 (1—14)	3 (30%)	3 (2—4)	3 (30%)	1 (1)	3 (30%)	—	17 (14—26)	
August	15	0 (0%)	—	4 (27%)	6 (2—10)	6 (40%)	2 (1—5)	3 (30%)	2 (1—4)	5 (33%)	—	19 (17—27)	
September	7	0 (0%)	—	3 (43%)	12 (1—32)	4 (57%)	2 (1—3)	2 (28%)	3 (2—4)	2 (28%)	—	18 (14—23)	
October	8	0 (0%)	—	1 (13%)	5 (5)	2 (25%)	1 (1)	2 (25%)	3 (1—5)	2 (25%)	—	21 (15—30)	
November	20	3 (15%)	2 (1—4)	15 (75%)	17 (2—76)	6 (30%)	2 (1—3)	6 (30%)	10 (1—36)	6 (30%)	—	19 (16—21)	
December	3	2 (66%)	2 (1—2)	1 (33%)	7 (7)	1 (33%)	2 (2)	1 (33%)	1 (1)	1 (33%)	—	26 (19—40)	
Total	124	18 (15%)	2 (1—4)	53 (44%)	33 (1—480)	41 (33%)	4 (1—19)	26 (21%)	4 (1—36)	4 (1—36)	—	20 (13—40)	

Table 2. Survey of the food of carp from the Mácha Lake fishpond system in 1981—82.

Month	Food
January	Relatively little food — mainly larvae of Chironomidae and Trichoptera
February	Masses of Ostracoda and larvae of Chironomidae
March	Digestive tracts of some carp empty, in others containing benthic invertebrates (mainly larvae of Chironomidae and snails)
April	Food mainly larvae of aquatic insects (Chironomidae, Trichoptera) and Ostracoda
May	Mainly larvae of aquatic insects (Chironomidae, Trichoptera, Ephemeroptera), Ostracoda and small Bivalvia, also individual beetles
June	Predominantly larvae of available Trichoptera, Chironomidae and some other Diptera, but also terrestrial insects (beetles); also small fishes (perch)
July	Mostly larvae of Chironomidae, also of Trichoptera, and small perch
August	Besides aquatic and occasionally terrestrial insects (Chironomidae, Ephemeroptera, ants) also clams (<i>Sphaerium</i>) and small fishes
September	Mainly aquatic insects (Chironomidae, Trichoptera) and <i>Sphaerium</i>
October	Mostly aquatic insects (Chironomidae, Trichoptera) and small clams (<i>Pisidium</i>), also Ostracoda and snails (<i>Bythinia</i>) rarely digestive tract of carp empty
November	Relatively little food — mainly larvae of aquatic insects (Chironomidae, Trichoptera) and Ostracoda and individual spiders
December	Digestive tracts empty, without food

corded in other fishes of this locality. The size of plerocercus is 0.680×0.258 mm; the length of larger hooks 0.30 mm, of smaller hooks 0.015 mm; the size of suckers $0.096 - 0.099 \times 0.060 - 0.081$ mm.

The development of this parasite involves two intermediate hosts: the first one are copepods (e.g. *Eudaptomus*) in which the larva attains the stage of cercoscolex, the second one are cyprinid fishes (frequently carp) in the gall-bladder of which the stage called plerocercus develops (Jarecka, 1970a); according to Bauer et al. (1981), in heavily infected fishes these larvae cause the disease, manifesting by their body length and weight retardation. As definitive hosts serve various fish-eating birds, mainly herons (*Ardea* spp.).

10. *Neogryporhynchus cheilancristrotus* (Wedl, 1855) — plerocerci (Fig. 4I, J)

Sporadic findings of these larval cestodes, localized in the anterior part of fish intestine, were recorded in young carp (body length 18—24 cm) in June, July and December (prevalence 2.4 %, intensity 1 plerocercus per fish). The body size of plerocerci was $0.422 - 0.465 \times 0.272 - 0.340$ mm, size of their suckers $0.084 - 0.090 \times 0.090 - 0.105$ mm; the length of larger hooks was 0.063—0.069 mm, of smaller hooks 0.045—0.048 mm. Besides carp, these larvae were also found in *Tinca tinca* (prevalence 2.6 %, intensity 1) in this locality.

The development of *N. cheilancristrotus* is similar to that of the foregoing species: copepods (e.g. *Mesocyclops*) serve as the first intermediate hosts, while the second ones are fishes, mainly cyprinids (Jarecka, 1970b). The cestode attains maturity in the gut of fish-eating birds (*Ardea* spp.).

Nematoda

11. *Pseudocapillaria brevispicula* (Linstow, 1873)

The bionomics of *P. brevispicula* in this locality has been dealt with in detail in a separate paper (Moravec, 1983). It can be concluded that this intestinal nematode is here the most frequent parasite of carp (prevalence 62 %, intensity 1–35); fish acquire new infections during the whole year and also mature nematodes are present in their fish hosts all the year round. However, the egg-producing females occur only in a warmer period from April until October, while the low water temperatures below 5 °C in November–March inhibit the normal development of eggs within the female uteri. Fig. 1D indicates that the highest values of prevalence are attained in carp smaller than 25 cm, this being partly reflected also by the values of mean intensity, while in larger fishes a gradual decrease in both prevalence and intensity takes place. The distribution of nematodes within the host fish population is only slightly overdispersed. In addition to carp, this parasite occurs also in *Tinca tinca* in this locality (prevalence 21 %, intensity 1–11).

The development of this pathogenic parasite, representing a possible danger to the intensive fish breedings, in particular of pond-reared carp, is not sufficiently known so far. It appears according to own observations that fishes become infected via freshwater oligochaetes serving as intermediate or paratenic hosts; a possible direct development of this parasite without intermediate hosts has been mentioned by Lomakin and Trofimenko (1982), but their data need to be verified.

12. *Raphidascaris acus* (Bloch, 1779) — larvae (Fig. 4C, D)

Larvae of this pathogenic parasite were sporadically found free in the intestine of medium-sized carp (length 20–24 cm) examined in February, March and May (prevalence 4.8 %, intensity 1–7). The length of larvae, representing evidently the third stage, ranged from 2.6–6.3 mm, maximum width was 0.068–0.122 mm; the most advanced larvae already possessed well developed lips. The larvae of *R. acus* were found, in addition to carp, also in *Abramis brama* (prevalence 29 %, intensity 1–1500), *Scardinius erythrophthalmus* (prevalence 13 %, intensity 1–2), *Rutilus rutilus* (prevalence 8.9 %, intensity 1–7), *Tinca tinca* (prevalence 4.6 %, intensity 1–3), *Esox lucius* (encysted larvae: prevalence 1.8 %, intensity 1–9), *Anguilla anguilla* (encysted larvae: prevalence 0.7 %, intensity 27) and *Perca fluviatilis* (prevalence 0.3 %, intensity 1).

Intermediate hosts of *R. acus* are various fishes, mainly cyprinids, while a number of invertebrates (largely larvae of Chironomidae and Oligochaeta) serve as the paratenic hosts of preinfective larvae (Moravec, 1970a); according to several authors (e.g. Supryaga and Mozgovoy, 1974) also invertebrates may function as intermediate hosts for *R. acus*. Taking into account that only free larvae of *R. acus* were found in the intestine of carp in the Mácha Lake pond system, it can be supposed that the main source of these infections in carp are incidentally ingested forage fishes — the intermediate hosts of *R. acus*; in this case carp would be a paratenic host. But neither the possibility of acquiring parasite's larvae by feeding on the invertebrates harbouring preinfective larvae can be excluded; if such larvae could develop further in the carp's intestine to attain their third stage, then carp would be the intermediate host for *R. acus*. As definitive hosts of *R. acus* serve some predatory fishes, in the locality under consideration mainly *Esox lucius* (prevalence 17 %, intensity 1–53), less frequently *Anguilla anguilla* (prevalence 3 %, intensity 1–2).

13. *Contracaecum microcephalum* (Rudolphi, 1809) — larva (Fig. 4A, B)

A single larva of this species was found in one young carp (body length 16 cm) (prevalence 0.8 %) examined in June 1981, being encapsulated on its gut-surface. The larva is 2.5 mm long and 0.177 mm wide. The mouth is formed by three rudimentary lips of which the dorsal one bearing a small, cone-shaped cuticular tooth. The cuticle is transversely striated, the width of annuli being 0.012—0.015 mm in the body region posterior to oesophagus. The oesophagus measures 0.456 mm, posterior ventricular appendage 0.489 mm, anterior intestinal caecum 0.270 mm, diameter of spherical ventriculus being 0.030 mm; the tail is conical. A larva of the same morphology was also found in the intestine of *Perca fluviatilis* (prevalence 0.3 %).

According to Mozgovoy et al. (1965) the first intermediate hosts of *C. microcephalum* are copepods of the genera *Cyclops* and *Macrocyclops*, while the second ones are various fishes, in which the larvae attain their third stage; in Europe the larvae occur mainly in cyprinids (Hartwich, 1975). As definitive hosts serve various species of fish-eating birds, particularly of the genera *Ardea*, *Ardeola*, *Nycticorax*, *Botaurus*, *Ixobrychus* and *Pelecanus*.

Although these larvae correspond both in their morphology and measurements to *C. microcephalum*, their assignment to this species without performing experimental feedings to definitive hosts is only provisional. It cannot be excluded that the larvae might belong also to *C. ovale* (Linstow, 1907), in which the larval morphology is inadequately known; adults of the latter species are, according to Hartwich (1975), parasitic in grebes (*Podiceps* spp.); these are as frequent as other species of fish-eating birds in the locality under consideration.

14. *Camallanus lacustris* (Zoega, 1776)

Single findings of *C. lacustris* were recorded from carp 20—23 cm long, examined in August and September (prevalence 2.4 %, intensity 1); the nematodes represented the fourth larval stage and young females, the most advanced of which (5.3 mm long) already possessed several eggs in its uterus; they were attached to the mucosa of the middle and posterior parts of the intestine. Apparently, carp become infected by *C. lacustris* by accidental ingesting small perch — the definitive hosts of this parasite. A possibility of the secondary infections of *C. lacustris* has been confirmed experimentally by Moravec (1971). Obviously, the nematodes do not develop in the carp's intestine, surviving there only shortly.

The life cycle of *C. lacustris* involves the intermediate host, various copepod species (Kupryanova, 1954, Campana-Rouget, 1961, Moravec, 1969); some fishes (e.g. cyprinids) may serve as paratenic hosts. Various piscivorous fishes, mainly perch, serve as the definitive hosts in the intestine and pyloric caeca of which this ovoviviparous nematode matures. In this locality the most frequent host is *Perca fluviatilis* (prevalence 71 %, intensity 1—38), but it occurs as well in *Stizostedion lucioperca* (in 1 of 2 fishes examined, intensity 17), *Anguilla anguilla* (prevalence 40 %, intensity 1—235) and *Esox lucius* (prevalence 44 %, intensity 1—23).

Acanthocephala

15. *Neoechinorhynchus rutili* (Müller, 1780)

This pathogenic parasite was found to be one of the most frequent parasites of carp under the conditions of the Mácha Lake fishpond system, where this fish species

serves as its principal host (prevalence 48 %, intensity 1–60). The seasonal occurrence and maturation of *N. rutili* in carp of this locality have been dealt with in detail in an earlier author's paper (Moravec, 1984a). It can be concluded that *N. rutili* exhibits a clear-cut annual maturation cycle in this locality when gravid females with mature eggs are present only in May; carp acquire new infections

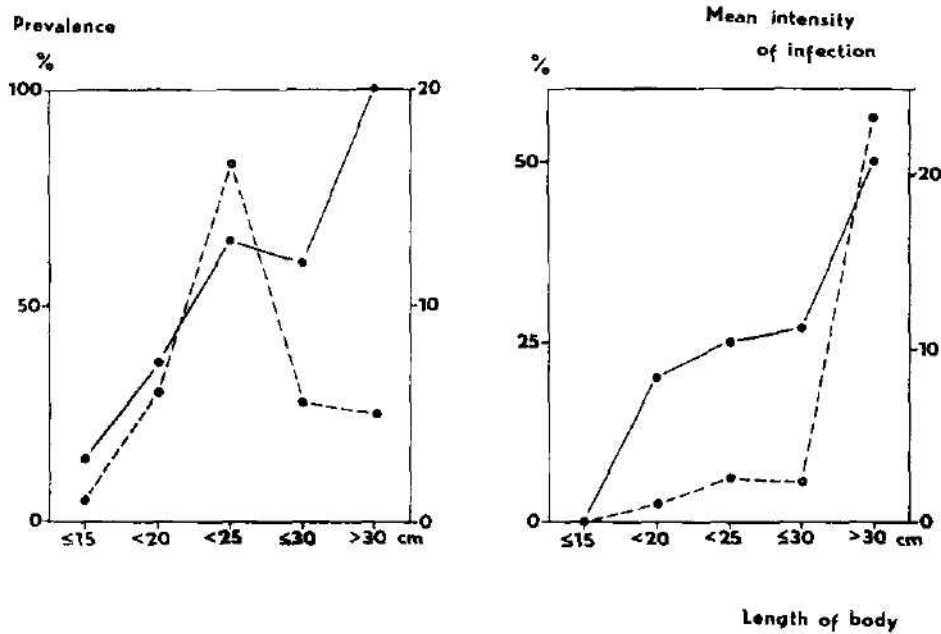


Fig. 3. Relationship of prevalence (— —) and mean intensity of infection (.....) to body length of carp: A — *Neoechinorhynchus rutili*, B — *Acanthocephalus lucii*.

from June until March of the next year, but mostly during autumn and early spring. This conspicuous seasonal cyclicality in *N. rutili* maturation and occurrence is mainly induced by the temperature regime in the locality, when namely higher water temperatures (above 20 °C) are applied, decreasing the ability of acanthocephalans to establish themselves in fishes during summer months. The highest values of prevalence and mean intensity of *N. rutili* in carp occur in a cooler season from October to March–April. The main source of infection for carp are the ostracod intermediate hosts, these being abundant in the locality; they were found in the diet of carp from autumn until spring. Fig. 3A indicates that infections are considerably influenced by the size of host fishes: while the prevalence rises along with the fish size attaining its maximum in the group of the largest carp, the mean intensity first increases with the fish size, reaching its maximum in carp 20–25 cm long, and then again decreases. Obviously, it is connected with the choice of food of larger carp in which, probably, the proportion of ostracods in the overall food volume is lesser than that in smaller ones.

Besides carp, also some other fish species were found to be hosts of these acanthocephalans in this locality, but no gravid females of the parasite were recorded in them: *Tinca tinca* (prevalence 2.9 %, intensity 1–13), *Gobio gobio* (prevalence

6.2 %, intensity 1), *Esox lucius* (prevalence 1.8 %, intensity 1) and *Perca fluviatilis* (prevalence 0.9 %, intensity 1–2).

The life cycle of *N. rutili* involves the intermediate hosts, various species of ostracods (Merritt and Pratt, 1964, Walkey, 1967); some invertebrates (e.g. leeches, megalopteran larvae) may obviously serve as paratenic hosts.

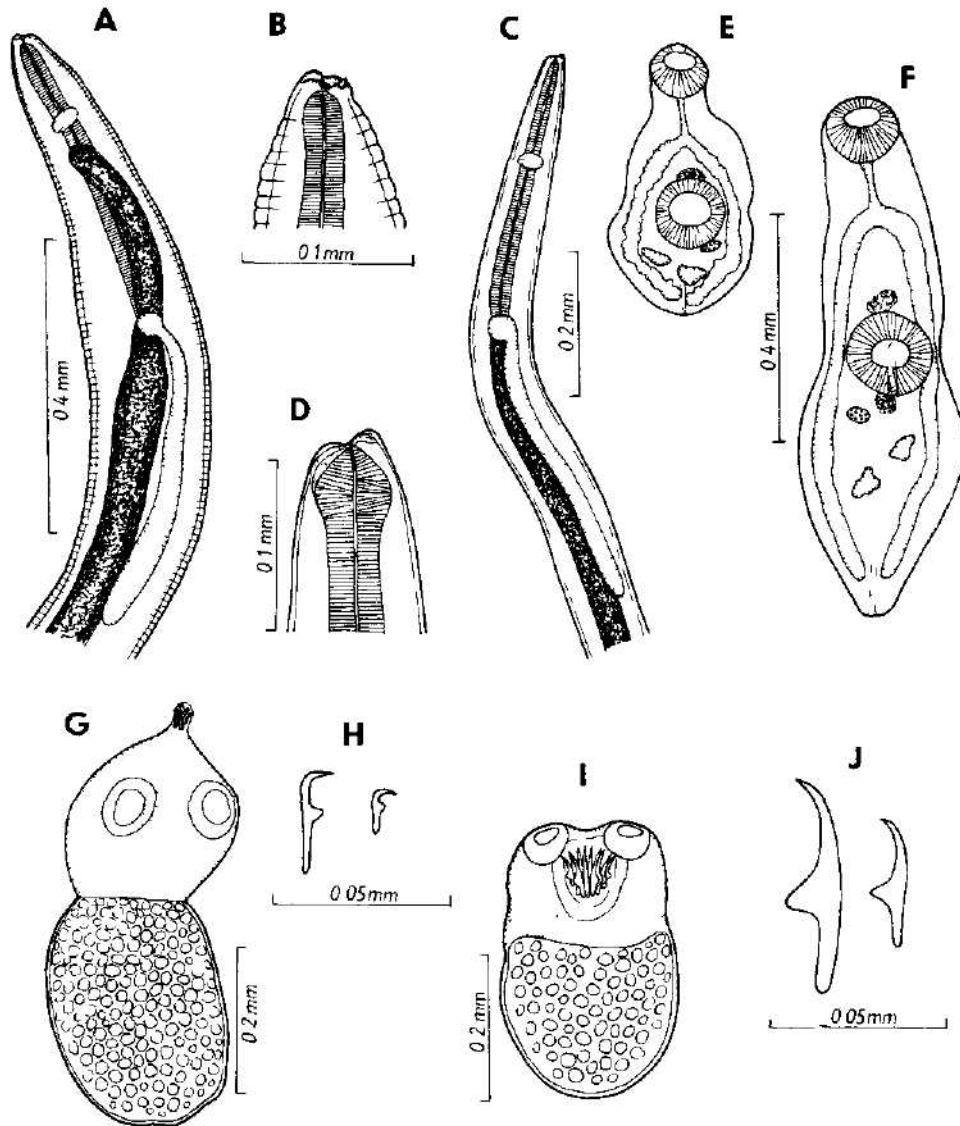


Fig. 4. Some helminth juveniles from carp of the Mácha Lake pond system: A, B — *Contracaecum microcephalum* larv. (anterior part of body and head end), C, D — *Raphidascaris acus* larv (anterior part of body and head end), E, F — *Phyllodistomum elongatum* juv. (E — specimen from intestine, F — specimen from urinary bladder), G, H — *Valipora campylancristroia* plerocercus (total view and rostellar hooks), *Neogryporhynchus cheilancristrotus* plerocercus (total view and rostellar hooks).

16. *Acanthocephalus lucii* (Müller, 1776)

This acanthocephalan was frequently found in the intestine of carp in this locality; the overall prevalence was 21 %, intensity 1–36 (average 4) specimens per fish. Different developmental stages of *A. lucii* were found practically during the whole year (except for January, March and April): males (length 3–6 mm), females still without eggs (length 6–12 mm), and in one case also two gravid females (length 9–10 mm) containing mature eggs were recorded in June; the acanthocephalans were mostly attached to the gut-wall of the host fish.

In the locality, the main hosts of *A. lucii* are *Perca fluviatilis* (prevalence 71 %, intensity 1–15), *Gymnocephalus cernuus* (prevalence 33 %, intensity 1–2), *Anguilla anguilla* (prevalence 31 %, intensity 1–18) and *Esox lucius* (prevalence 63 %, intensity 1–53) in which acanthocephalan females attain gravidity; it was also found in *Tinca tinca* (prevalence 4 %, intensity 1–4), *Abramis brama* (prevalence 2.5 %, intensity 1–8) and *Gobio gobio* (prevalence 5 %, intensity 1). Apparently, carp as well as other cyprinids do not serve as the definitive hosts of *A. lucii*, in which the parasite becomes gravid, but only as either postcyclic hosts acquiring invasions secondarily while feeding on other fishes (e.g. perch), or paradefinitive hosts, when invaded intermediate hosts (freshwater isopods) are swallowed up.

It is obvious from Fig. 3B that *A. lucii* infections in carp are in a distinct relation to the body size of hosts: infections were only found in carp larger than 15 cm; both prevalence and mean intensity of *A. lucii* decrease with the host's size to attain their maximum in largest carp (above 30 cm). It suggests that forage fishes (perch) are the main source of *A. lucii* infections for carp.

It was found earlier (Moravec, 1979a) that in pike of this locality *A. lucii* did not exhibit a distinct seasonal maturation cycle and gravid females of this parasite occurred in *E. lucius* throughout the year. The freshwater isopod *Asellus aquaticus* was found here to be the intermediate host of *A. lucii* (see Moravec, 1979a); the juvenile acanthocephalans obtained from the body cavity of these crustaceans during March and May represented in fact young males (length 4–5.5 mm) and females with already developed ovarian balls (body length 5–6 mm).

CONCLUSIONS

A revision of the extensive domestic literature dealing with the parasites of carp (*C. carpio* L.) has revealed that a total of 24 species of endohelminths (Trematoda 11, Cestoda 7, Nematoda 2, Acanthocephala 4) has so far been recorded from this commercially most important fish in Czechoslovakia; these data concern the carp both from pond breedings and open and standing waters (rivers, pools, lakes, man-made water reservoirs). In the Mácha Lake fishpond system altogether 16 species were found, this giving evidence, in comparison with the above data, for a rich fauna of endohelminths in this locality. Of the endohelminths reported from carp in Czechoslovakia, only 6 species of trematode metacercariae, 3 species of cestodes and 2 species of acanthocephalans were not found there; however, most of them have been reported from natural waters only, not from fishponds. On the other hand, 5 species are recorded here for the first time from carp in Czechoslovakia: *Proteocephalus percae* juv., *Triaenophorus nodulosus* juv., *Camallanus lacustris*, *Acanthocephalus lucii* and *Contracaecum microcephalum* larvae; the first species is recorded for the first time in a cyprinid fish, while the latter represents the first documented finding of *Contracaecum* larvae in fishes of Czechoslovakia. More than one half of

the 16 recorded species of parasites is represented by larval stages (7) or juvenile forms (2), whereas only 7 species were recovered as adults.

Analysis of the parasites indicates that these can be roughly divided into four groups according to the degree of their host specificity: 1. strictly specific species occurring only in carp (*A. carparum*, *S. inermis*), 2. species occurring as well in other cyprinids (*Ph. elongatum*, *C. fimbriceps*, *P. brevispicula*), 3. species occurring also in fishes of other families, for which carp is an obligate host (*D. spathaceum*, *C. pileatus*, *V. campylancristrota*, *N. cheilancristrotus*, *C. microcephalum*, *N. rutili*), and 4. species developing in other fishes than carp, the latter serving for them as only a facultative host in the intestine of which these worms can survive for a certain time after their original obligate host was swallowed up and digested (*P. percae*, *T. nodulosus*, *R. acus*, *C. lacustris*, *A. lucii*); while carp is either the intermediate or definitive host for parasites of the first three groups, for helminths of the last group it can serve as only a paratenic, postcyclic and probably also paradenitive host according to the conception of Odening (1976). It is obvious from the comparison of individual groups that most species (11) are obligate parasites of carp, this being for 4 of them the only or the principal host, while the group of facultative parasites is represented by only 5 species. The proportion of facultative parasites of carp is low in comparing, for example, with pike; in the latter fish those species prevail, for which it serves as only a facultative host (Moravec, 1979a); this reflects widely different ways of nourishment in the two fish species, because while larger pike are exclusively piscivorous, carp feed mainly on invertebrates, ingesting small fishes incidentally; the species composition of facultative parasites of carp indicates that all of them are probably obtained by carp while feeding on small perch. Small perch occur in masses in this locality (mainly in the interconnecting canal) and their remnants were sometimes found in the intestine of examined carp (see Table 2).

It is obvious from Figs. 1 and 3 that there are distinct differences in the rates of infestation among individual size groups of carp; however, this comparison concerns only the six commonest species, while it was not possible to compare these data in the remaining species due to their rare occurrence in carp. The found differences are both qualitative and quantitative: while in carp with body length of 15–30 cm all the 6 parasite species were present, in the smallest carp (below 15 cm) one species (*A. lucii*) was absent as also in the largest carp (above 30 cm) (*D. spathaceum*). Quantitative differences concern the values of prevalence and mean intensity of infection; here it is possible to distinguish four main groups of species: a) species with the prevalence and mean intensity increasing along with the host's body (*A. lucii*), b) species with the prevalence increasing with the host's size and with the values of mean intensity first increasing and then, after attaining its maximum, again decreasing (*A. carparum*, *N. rutili*), c) species in which both the values first increase until a certain size of carp is attained and then again fall (*D. spathaceum*, *P. brevispicula*), and d) species with irregularly fluctuating values of prevalence and mean intensity of infection (*S. inermis*). All these growth changes in the helminthofauna are associated with the life cycle pattern of each parasite, the source of infection for carp, the ecology and ethology of host fish and probably also with the degree of defence reactions in the individual age groups of carp.

As far as the way of infection in carp is concerned, it is obvious that except for the 3 trematode species whose cercariae penetrate actively into the fish (*S. inermis*, *D. spathaceum*, *C. pileatus*), invasions by all remaining helminths are acquired by fish *per os*, while swallowing up free invasive stages of the parasite (*Ph. elongatum*), invaded invertebrates (e.g. *A. carparum*, *C. fimbriceps*, *V. campylancristrota*, *P. bre-*

vispicula, *N. rutili*) or forage fishes (e.g. *P. percae*, *C. lacustris*, *A. lucii*). Accordingly, a choice and a composition of carp's food is very important for the formation of the helminthofauna in this fish species, this being considerably influenced by local ecological conditions (Table 2). A mass occurrence of small perch in the locality and their easy availability to carp are reflected by the composition of the helminthofauna of these fish; occurrence of the endohelminths typical of perch has not been hitherto recorded from other localities in Czechoslovakia, although it is well-known that carp feed occasionally on small fishes. The significance of local ecological conditions for the formation of the carp helminthofauna is also manifested by the presence of a considerable number of larval helminths maturing in fish-eating birds (*D. spathaceum*, *C. pileatus*, *V. campylancristrotus*, *C. microcephalum*); these species are usually found in carp mostly in natural waters under the conditions of Czechoslovakia, being relatively rare in pond-reared carp; the presence of these larval stages in carp of the Mácha Lake fishpond system is conditioned by a considerable richness of the local fauna of waterbirds.

It is known for many fish helminths that their occurrence in the host or their maturation are subjected to seasonal changes; despite the high practical significance of such data the present knowledge is in this respect inadequate. Of the parasites recorded from the Mácha Lake fishpond system, seasonal changes in occurrence and maturation could be considered in 5 species only (*S. inermis*, *A. carparum*, *D. spathaceum*, *P. brevispicula*, *N. rutili*); all these species occur in carp during the whole year. Out of these species, a pronounced seasonal cycle of maturation was found only in *N. rutili*, whose gravid females occurred here only in May, and a partial seasonality in maturation was observed in *P. brevispicula*, in which the oviposition took place during the whole warmer season from April until October; on the other hand, *A. carparum* did not exhibit seasonality in maturation and both the egg-production and recruitment were recorded during all seasons: egg-production of *S. inermis* was not followed

Of the endohelminths recorded in the Mácha Lake fishpond system, as the most serious parasites of carp appear the acanthocephalans *Acanthocephalus lucii* and mainly *Neochinorhynchus rutili* which may very negatively affect the health condition of the infected fishes and may be the cause of their mortality (e.g. Štědronský and Pekař, 1954, Bauer et al., 1981), as also the trematode *Allocreadium carparum*, occurring here in carp in large numbers and whose pathogenicity has not been elucidated so far. The other pathogenic species, *Sanguinicola inermis*, *Diplostomum spathaceum*, *Valipora campylancristrota* and *Pseudocapillaria brevispicula*, well-known causative agents of the serious diseases of pond fishes, occur in carp of this locality in small numbers only, it is due to the present-day ecological conditions in the locality, but for the future, these species represent a certain danger to carp breeding and under the changed ecological conditions (e.g. fish stock composition and density) they might be the cause of considerable economic losses.

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**POPULATION NUMBERS AND CHANGES OF THE PRODUCTION AND YIELD
OF THE ROACH WITH RESPECT TO THE ORGANISATION OF THE FISHERY**

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Abstract. The size of population of the roach in the Klíčava reservoir in 1977–1983 was estimated on the basis of relations between the rate of exploitation and fishing mortality. The values of the estimates for the years 1977 to 1979 were compared with the estimates by Schnabel. The population number of younger age groups (2.–5.), which do not participate completely in the spawning, was corrected by estimating the recruitment coefficient. A simple simulation model was employed to follow a relationship between the production and yield for two types of fisheries. Particular combinations of these relationships are discussed.

INTRODUCTION

Marking of fishes and the analysis of the ratio of marked and unmarked fishes in subsequent catches has been traditionally used to estimate the size of population of fishes in the Klíčava reservoir. Marking of a larger portion of fishes is provided in the spring, when sexually mature individuals are accumulated in shore areas and thus can be easily caught. In the spring period, it is also possible to recapture the largest number of the marked fishes. With respect to the fact that it is impossible to catch and mark sufficient number of fishes in one period, it was necessary to accumulate marked fishes in subsequent period. So, in the course of the experiment, the number of marks continually increased, as assumed in the method by Schnabel.

In the Klíčava reservoir the method has been used several times (Oliva, Holčík, 1965; Holčík, 1970; Pivnička, 1982). Different types of marks from 1977, 1978 and 1979 were used to obtain estimates of the population number in these years and simultaneously for estimates in 1980 to 1983, when the marking procedure was not performed. A correction of the estimates was carried out considering the fact that part of the fishes of younger age groups do not participate in spawning— the estimates are lowered. With a help of a simple analytical model, a relationship was demonstrated between a change of the values of the production, yield and intensity and type of the organisation of the fishery.

MATERIAL AND METHODS

The Klíčava reservoir lies in Central Bohemia, the average area being of 55 ha. For a detailed description of the reservoir see Holčík (1977).

The method of estimating the population number of the roach used in this work again employs subsequent catches. The coefficient of exploitation (u) was estimated on the basis of the ratio between the total number of marked fishes in the reservoir and number of recaptured marked fishes. When assuming the value of the instantaneous coefficient of the natural mortality at the time of estimates to be low, and the decrease of the number of fish to be due only to fishing

Table 1 Basic data necessary for estimating the population number of the roach in 1977—1979.
 C_i — actual catch, M_i — number of marked fish from the catch "i", M_{i0} — total number of marked fish in the reservoir before the catch "i",
 $R_{i(rv)}$, $R_{i(iv)}$, $R_{i(D)}$ — number of recaptures marked by clipping of right ventral (1977), left ventral (1978) and dorsal (1979) fin, respectively,
 F_i — instantaneous fishing mortality

1977										1978										1979									
Date	C_i	M_i	M_{i0}	$R_{i(rv)}$	F_i	Date	C_i	M_i	M_{i0}	$R_{i(rv)}$	$R_{i(iv)}$	F_i	Date	C_i	M_i	M_{i0}	$R_{i(rv)}$	$R_{i(iv)}$	$R_{i(D)}$	F_i									
21. 4.	52	52	—	—	—	9. 5	65	19	—	3	—	—	3. 5.	44	44	—	1	2	—	—									
28. 4.	71	67	52	—	—	13. 5.	140	117	19	4	—	—	11. 5.	101	99	44	3	6	—	—									
5. 5.	134	116	119	—	—	17. 5.	+290	238	136	6	3	0.022	17. 5.	+417	384	143	10	14	2	0.014									
13. 5.	+412	368	235	1	0.0043	25. 5.	+618	545	374	28	7	0.019	22. 5.	+998	648	527	27	39	18	0.035									
17. 5.	+709	597	602	13	0.023	1. 6	+101	80	971	3	1	0.001	30. 5.	+32	14	1173	4	—	6	0.005									
$\Sigma C_i = 1121$, $\Sigma F_i = 0.0293$ $N = 38\ 660$, $\Sigma M_{i(rv)} = 1\ 421^{++}$ Schnabel's estimate = 33 991										$\Sigma C_i = 1\ 009$, $\Sigma F_i = 0.041$ $N = 24\ 020$, $\Sigma M_{i(iv)} = 1\ 188^{++}$ Schnabel's estimate = 24 839 $\Sigma R_{i(rv)} = 881$, $S_{iv1977-78} = 0.62$										$\Sigma C_i = 1\ 477$, $\Sigma F_i = 0.053$ $N = 27\ 301$, $\Sigma M_{i(D)} = 1\ 295^{**}$ Schnabel's estimate = 20 983 $\Sigma R_{i(rv)} = 773$, $S_{iv1978-79} = 0.84$ $\Sigma R_{i(iv)} = 1\ 000$									

+ catches when estimates of F_i were possible
 ++ together with fish marked in summer and autumn

Table 2 Total number of recaptured fishes marked by clipping of the right ventral, left ventral and dorsal fin R_{RV} , R_{LV} , R_D , number of recaptured per 1000 fishes (r_{RV} , r_{LV} , r_D), survival S calculated on the basis of different types of marks. The total number of marked fishes surviving to the following year ΣR , coefficient of exploitation 'u' and values of estimates in years 1979—1983

	1979	1980	1981	1982	1983
R_{RV}/r_{RV}	50/28.6	20/14	10/5.3	5/2.2	1/1.4
R_{LV}/r_{LV}	64/36.6	26/18.2	13/6.9	18/6.7	2/2.7
R_D/r_D	—	35/24.5	37/19.6	40/16.1	5/6.8
$S_{RV, LV}$	0.49	0.37	0.72	0.46	
S_D	0.63	0.80	0.82	0.42	
$\Sigma R_{RV, LV}$	1 773	878	324	233	107
ΣR_D	1 295	813	650	533	224
u		0.043	0.06	0.087	0.024
N	27 301	33 162	31 416	35 793	30 583

mortality, then the estimate of the instantaneous coefficient of the fishing mortality F_1 for each period (1) may be performed using the following relationship:

$$R_1 = M_{01} \cdot F_1 \int_{t_1}^{t_2} e^{-F_1 t} dt = M_{01} (1 - e^{-F_1 (t_2 - t_1)}) \quad (1)$$

where M_{01} — total number of marked fishes at the time just before fishing, R_1 — number of marked individuals recaptured in a period $t_2 - t_1$. Equation (1) enables to estimate on the basis of known values M_{01} and R_1 partial values of F_1 and last also a total value of the instantaneous coefficient of the fishing mortality- F for the period of interest (regardless the fishes are released into the water or not). This enables us to estimate values of the coefficient of exploitation (u) which is in a relation with F , the dependence being of the type $u = 1 - e^{-F}$.

The final estimate of the population size can be then performed on the basis of a known relationship $u = C/N$, where C is a number of fishes caught in the whole period, N is the population size to be determined.

The method of the estimation mentioned, which represents a certain modification of the estimate by Schnabel, was used to estimate the population number of the spawning shoal of the roach in 1977, 1978 and 1979. The fishes were marked by fin clipping (right ventral in 1977, left ventral in 1978 and dorsal fin in 1979). In 1977—1979 all fishes were released into the water, in 1980—1983 they were all removed. In Table I data are summarized necessary for estimates by the mentioned modification, including data about the values of the population size obtained by a method by Schnabel (Pivnička, 1982).

In 1980, 1981, 1982 and 1983 the marking of fishes did not continue and thus, the estimate according to Schnabel was impossible. However, recaptured fishes marked in preceding years were recorded. In these years the population size was accomplished on the basis of the fish survival (S_j), calculated from the relationship $S_j = \frac{r_j}{r_{j-1}}$, where r_j and r_{j-1} stand for return of marks per 1000 caught fishes in subsequent years. The exploitation coefficient for a given year (j)

can then be calculated from the equation $u_j = \frac{R_j}{M_{j-1} \cdot S_j}$ where R_j is a total number of returned marks in a year j , M_{j-1} is a total number of marked fishes in the reservoir in the preceding year. When estimating the survival in a given period (1980—1983) on the basis of returns of marks from 1977 and 1978 they were necessarily combined because of a low rate of recapture, and for the estimate of the survival as well as exploitation coefficient an arithmetic mean, calculated from both types of marks and of marks from 1979 was used, Table 2.

The value of the instantaneous growth coefficient (G) (starting with the second age group) was calculated using the last observed value of the weight of each age group and preceding back estimated weight (Ricker, 1969). The estimate of the mean annual biomass (\bar{B}) was provided according to Ricker, 1975 on the basis of equation

Table 3. Population number of the roach in particular age groups estimated on the basis of the age composition of the population in 1977-1982, AG - age group

Age group	1977	1978	1979	1980	1981	1982
2						
3	10 780	360	4 258	2 355	2 170	11 645
4	3 125	8 682	2 380	13 530	3 308	2 159
5	6 378	2 418	9 516	3 285	13 744	3 007
6	12 729	4 410	1 856	1 829	2 658	9 947
7	3 363	6 348	3 855	6 769	1 120	2 113
8-∞	2 284	2 802	5 434	972	3 833	885
				4 322	4 583	6 037
N	38 660	24 020	27 301	33 162	31 416	35 792

Table 4. The values of recruitment, P_i (2nd-5th AG), calculation procedure see in text

Age group	1977	1978	1979	1980	1981	1982
2						
3						
4	10 780	360	4 259	2 355	2 170	
5		1 988	2 078	13 530	1 919	450
			2 223	857	5 761	
				572	720	
1977	$N_3 = 10\ 780 + 1\ 988/(0.62 + 2\ 223/(0.62 \cdot 0.84)) = 18\ 271$					
1978	$N_3 = 360 + 2\ 078/0.84 + 572/(0.84 \cdot 0.57) = 4\ 028$					
1979	$N_3 = 4\ 259 + 857/0.57 + 720/(0.57 \cdot 0.59) = 7\ 803$					
1980	$N_3 = 13\ 530 + 5\ 761/0.59 = 23\ 294$					
1981	$N_2 = 2\ 355 + 1\ 919/0.59 + 459/(0.59 \cdot 0.77) = 6\ 618$					
1982	$N_2 = 2\ 170 + 488/0.77 = 2\ 804$					

$$\bar{B} = \sum_{i_0}^{i_x} B_{0i} \frac{e^{G_i - Z_i} - 1}{G_i - Z_i} \quad (2)$$

for a case, when the catch of fish is extended throughout the year and according the expression

$$\bar{B} = \sum_{i_0}^{i_x} B_{0i} e^{-P} \cdot \frac{e^{G_i - M_i} - 1}{G_i - M_i} \quad (3)$$

for a case when the fishery is concentrated into one time at the beginning of the vegetation period, where M_i is the instantaneous coefficient of the natural mortality.

The equation for the yield estimate for corresponding two cases are in the following forms

$$Y_1 = \sum_{i_0}^{i_x} F \bar{B}_i \quad \text{and} \quad Y_2 = \sum_{i_0}^{i_x} B_{0i} (1 - e^{-P}) \quad (4)$$

respectively, where B_{0i} is biomass of the i -th age group at the beginning of the season (at the spawning time), G_i and Z_i are instantaneous coefficients of the weight growth and total mortality, respectively, i_0 and i_x are the youngest and oldest age group in the population considered.

The annual production, including the weight increase by those fish, who did not survive till the end of the year was estimated according to equation

$$P = \sum_{i_0}^{i_x} \bar{B}_i G_i \quad (5)$$

RESULTS

From estimates of the population size of the spawnings shoal of the roach in 1977 to 1982 it can be seen that these numbers do not agree with an estimated level of the survival of particular age groups of the spawning shoal. This disagreement is primarily in a connection with different strength of the recruitment and it may be supported by an analysis of the age structure of the spawning shoal in the years of interest (Table 3).

Here, it is to remind that the character of structures on scales of the roach (particularly older ages) and also their low number in samples rather complicate precise estimates of the age composition. For this reason, all fishes of 8 years and older were put into one group of "old fishes".

Starting from 1980 the haul seine was also used for catching the roach in the Kličava reservoir, which extended the spectrum of captured length groups, particularly of the second age group.

Table 3 clearly indicates disagreements of population estimates of subsequent age groups in certain years, which could be expected on the basis of estimated survival coefficients. In two cases, the population number in an older age group in the sequence of the generation was early increased as compared to the situation one year ago. The fact that the disagreement in the population number of subsequent age group occurs particularly in younger age groups indicates a continuous sexual maturation of the roach and entering into the spawning shoal. The fact that the maturation is not concentrated into one year complicates estimates of the population number, biomass, as well as production of the roach and calls for a correction of the population number of younger age groups.

This correction can be accomplished in cases where the survival coefficient is known and further, where spawning is not omitted starting from a certain age group (i.e. by sexually mature individuals) and where it is possible to determine the age of terminating the completion of the population, i.e. the age from which all the individuals participate in spawning.

Table 5. Reconstructed population number of roaches.
 Values marked by + were completed using values of the recruitment, those marked by ++ were reconstructed with the help of survival values, AG — age group, B — biomass, P — production

Age group	1977	1978	1979	1980	1981	1982
2	6 497++	9 408+-	40 867++	6 618+	2 804+	11 645
3	18 271+	4 028+	7 903+	23 294+	3 904+	2 159
4	3 126	11 328+	3 384+	4 505+	13 744	3 007
5	6 378	2 418	9 516	1 929	2 658	9 947
6	12 729	4 410	1 856	6 769	2 210	2 113
7	3 363	6 348	3 855	972	3 833	855
8—∞	2 284	2 802	5 434	4 322	4 583	6 037
Total						
2AG—∞	52 648	40 742	72 815	48 409	32 646	35 739
Total						
3AG—∞	46 151	31 334	31 948	41 791	29 842	24 148
3AG—∞ . . ha ⁻¹	839	570	581	760	543	439
B 2AG—∞ kg.ha ⁻¹	138.2	106.9	128.8	113.9	94	90.6
P 2AG—∞ kg.ha ⁻¹		40.4	69.1	55.1	33	33

The annual survival rate may be assessed on the basis of the analysis of returns of marked fishes. There are no demonstrations that the roach in the Klíčava reservoir omits spawning. Last there is no problem with establishing the age of terminating the process of the completion of the population — this is an age from which a further development of the population number of the generation agrees with estimated values of the survival (these age groups are marked with an asterisk in Table 3).

We will denote by N_i the total population number of an age group at a time immediately preceding its entrance into the spawning shoal (in a given case $i = 3$ for a period of 1977 to 1979 and $i = 2$ for 1980 to 1982). Symbols $S_i, S_{i+1}, S_{i+2} \dots$ stand for survival of this age group in the given and subsequent years, respectively, and symbols $X_1, X_{i+1}, X_{i+2}, \dots$ for coefficients of recruitment, i.e. ratio of the population number of individuals achieving their sexual maturity at the age (i) to the total population number of the generation in the corresponding year. On the basis of data from Table 3 and calculated values of the survival coefficient it is possible to estimate the value of the recruitment, which is formed from those individuals of each age group in particular years up to its complete entrance into the spawning shoal (i.e. when all the individuals achieve their sexual maturity). This value of the recruitment (P_i) is nothing else than a difference between the actual (N_i) and expected ($N_{i-1} \cdot S$) population number of sexually matured individuals of a corresponding age group in year "i", i.e. $P_i = N_i - (N_{i-1}/S_i)$ (Tab. 4.) The values P_i may also be expressed with the help of known relationships characterizing the dynamics of the population number of sexually matured individuals of a given age group. So, for already mentioned case

$$P_3 = N_3 \cdot X_3$$

$$P_4 = N_3 \cdot S_3(1 - X_3) \cdot X_4$$

$$P_5 = N_3 \cdot S_3 \cdot S_4 (1 - X_3) (1 - X_4) \cdot X_5$$

$$P_6 = N_3 \cdot S_3 \cdot S_4 \cdot S_5 \cdot (1 - X_3) (1 - X_4) (1 - X_5) \cdot X_6$$

As mentioned above, these relationships hold only in a case where sexually mature individuals do not omit spawning. It is obvious that the value P_i approaches zero when a given age group enters continuously into the spawning process as whole. This also means that $X_i \rightarrow 1$. The end of completing the generation starts at different times, at different ages in different years. It is not difficult to imagine that in cases, where the formation of the spawning population terminates simultaneously in a year where the generation enters into the spawning shoal, i.e. when $X_3 = 1$ simultaneously $P_3 = N_3$ as far as the completion takes a further year ($X_4 = 1$), then

$$N_3 = P_3 + P_4/S_3 \text{ when the completion takes two years, then}$$

$$N_3 = P_3 + P_4/S_3 + P_5/S_3 \cdot S_4 \text{ when it takes three years, then}$$

$$N_3 = P_3 + P_4/S_3 + P_5/S_3 \cdot S_4 + P_6/S_3 \cdot S_4 \cdot S_5, \text{ etc.}$$

A corresponding calculation, whose results are summarized in Table 4 may be illustrated by way of an example of the reconstruction of the population number of a generation, whose members became first into the spawning generation in 1978. On the basis of data from Table 3 it is possible to determine values P_i ($P_3 = 360 - (N_{i-1}) \cdot 0.62$), the value of the term (N_{i-1}) equals zero, since a number of sexually mature roaches in 2 AG equals zero, $P_4 = 2380 - 360 \cdot 0.84 = 2078$, $P_5 = 1929 - 2380 \cdot 0.57 = 572$. From this table it is also possible to see that the process of completing the population terminates at an age of five years (subsequent values of estimates of sexually mature fishes starting from the fifth age group are in a good agreement with values obtained on the basis of average values of the survival. In agreement with the above procedure we have:

$$N_3 = 360 + 2078/0.84 + 572/0.84 \cdot 0.47; \text{ and hence}$$

$$N_3 = 4028$$

The density of the roach (AG 3- ∞) ranges between 439 and 839 individual per ha (Table 5) and tends to decrease in a comparison with preceding years. The mean density in 1963-1979 was of 846 roaches $\cdot \text{ha}^{-1}$ (Pivnička, 1982).

Model

As already mentioned, there are attempts to consider the annual production as an indicator of a possible yield (Rudenko, Umnov, 1982). In connection with this, attention should be paid to changes of the yield and production of the population depending on the intensity and character of the fishery (Ricker, 1975). However, possibilities of this analysis on the basis of actual values are very limited. For this reason, a method of the imitation modelling was used in the present work. The proposed model takes into consideration the dynamics of the population size and biomass of one generation of the roach in the course of its whole life starting from the second age group. The yield and production (equations 2-5) was followed for different values of the instantaneous coefficient of the fishing mortality (from 0 to 5 with a step of 0.1).

The initial population size and weight of individuals was considered to be constant ($N_2 = 20\,000$, $w_2 = 29$ g) and changes of both parameters in a generation was described by exponential function as follows from equations 2 and 3. Further we assume the values of instantaneous coefficients of the natural mortality to be unambiguously determined by the age of individuals. In one variant of the model, instantaneous

Table 6. Parameters of the model:

N — initial abundance, w — weight in g, M_1 — instantaneous coefficient of the natural mortality, G_1 — instantaneous coefficient of the weight growth, NN — abundance for which the growth rate (G_1) is retarded twice

Age group	N	w	M_1	G_1	NN
2	20 000	29	0.28	1.15	18 000
3			0.28	0.9	14 000
4			0.28	0.42	10 000
5			0.28	0.3	7 500
6			0.28	0.16	5 500
7			0.7	0.14	3 000
8			1.6	0.10	2 000
9			1.6	0.07	500

coefficients of the weight growth were also constant, in the second variant the effect of the population number of the roach on its growth was taken into account. In a connection with this, in the second variant values of instantaneous coefficients of the weight growth were corrected by

$$Cor_1 = NN/N_1 + NN,$$

where NN is a mean annual population size of a generation, for which the rate of weight growth is retarded just twice, N_1 is a given estimated number of this generation (for $N_1 \rightarrow NN$, $Cor_1 \rightarrow 1/2$; for $N_1 \rightarrow 0$, $Cor_1 \rightarrow 1$)

To particular parameters of the model probable values were assigned (Table 6). They were obtained in the course of this work as well as in the preceding studies of the roach population in the reservoir.

Figs. 1, 2 show changes of the yield and production values of the 2nd age group obtained during the run of the model. Corresponding values of the yield and production may also be interpreted as an annual yield and production of the population with a constant recruitment.

As can be seen from presented graphs, both considered situations exert a mutual decrease of the production with increasing the yield. The yield curves have a maximum corresponding to a certain value of the fishing mortality (F). The mentioned character of the dynamics of the fishery does not need further explanation, since the presented relationships are sufficiently known (Baranov, 1918; Beverton, Holt, 1957). However, it is necessary to stress that the production of the generation studied, for values of F lower than those which could provide a maximum yield, is essentially higher (particularly in a variant with the density-dependent growth) than the yield that can be obtained (and maintained) at a stable level. For this reason the interpretation of the production as a measure of a possible yield is rather unreliable.

Results of accomplishing the first variant of the model without the density dependent regulation of the growth make it possible to see different values of the yield and production conditioned by the character and organisation of the fishery. It is shown that the yield as well as production are lower in the case of the type 1. fishery when the natural mortality occurs after fishing ends, than in the case of organizing the fishery for the whole season (type 2 fishery) when the natural and fishing mortality operate concurrently see Rieker, 1975. This fact suggests that the continuous fishery of the same intensity provides a larger average biomass and production of the population. With increasing the fishing effort this difference is ever increased.

particularly thanks to a relative increase of the abundance of younger age groups, where an increase of the biomass during the season is mostly positive, Fig. 1.

A rather different situation occurs when accomplishing the second variant of the model, where a negative dependence of the growth on the population size was mediated. Besides an expected increase of the values of the followed parameters, there

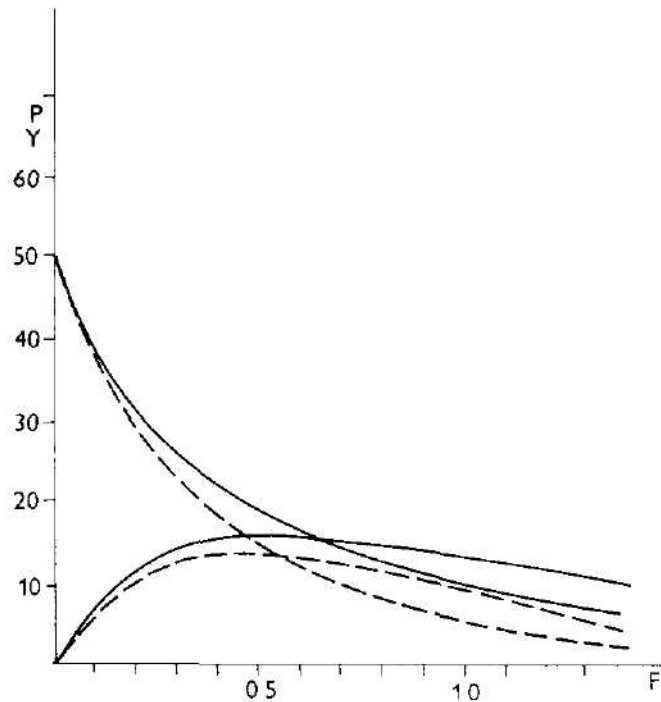


Fig. 1. Dynamics of the yield and production (Y,P, kg ha⁻¹) for different values of fishing effort (F). Solid line — yield and production for a continuous fishery (organized for the season), dashed line — the same for the single fishery — organized in a short time (at the time of spawning).

is also an obviously different relationship between them. The yield achieved during the type 1. fishery is higher than that during the type 2. fishery (Fig. 2) above all for low and medium values of F. This should be taken into account for economically optimal organisation of fisheries. For lower values of F the production under conditions of the type 1. fishery is also rather high but stepwise, with increasing of F, the production and yield are higher in the 2nd type of fishery.

The population control of the weight growth provides a larger increase of the biomass at lower and medium values of F in a case when catch is organized as a type 1. fishery only at the beginning of the season. However, in the case of a remarkable intensification of fishing effort (often uselessly under real conditions) compensation possibilities of the population are depleted, so that it is impossible to expect that increases in the weight growth compensate low abundance.

Values of the yield in this variant approach values of the production only for an intensity of the fishery $F \geq 1.2$, $u \geq 0.48$. Those are values higher by a factor of

five than those achieved in the Kličava reservoir (they correspond to 100–120 kg of fishes per ha annually).

DISCUSSION

The mentioned procedure of the reconstruction of abundance makes it possible to obtain not only a corrected estimate of the population number in a given and subsequent years, however, also an estimate of recruitment coefficients, which are

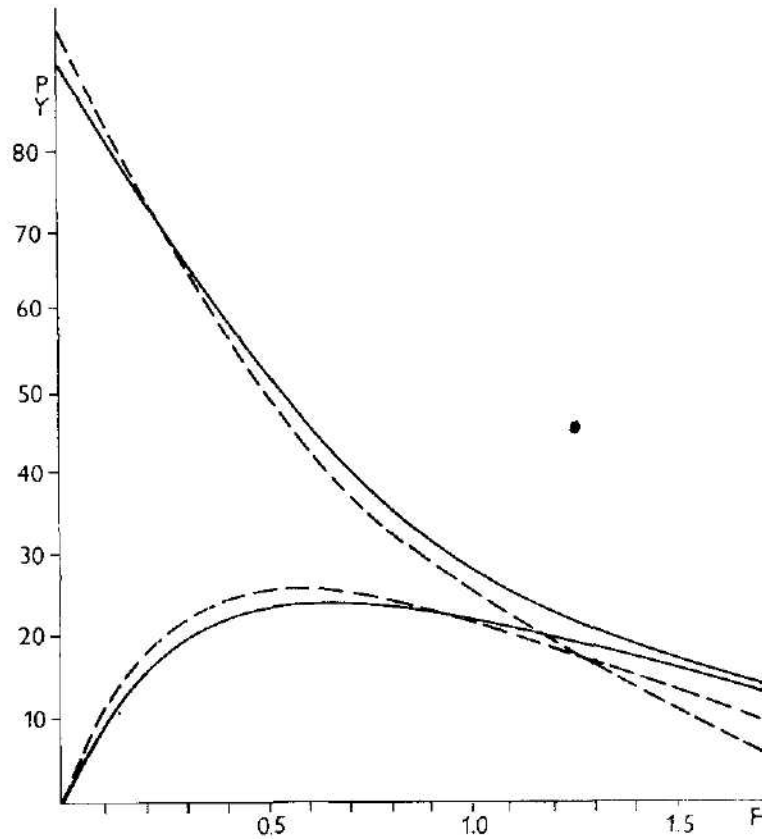


Fig. 2. The same as in Fig. 1. with considering the density dependent regulation of the growth.

necessary to assess the process of the sexual maturation of fishes. It is also of importance, that the introduced method of the reconstruction of the population size of younger age groups may be used independently of what factors affect their incomplete presence in the estimated population — either continuous sexual maturation or selectivity of the nets used.

Estimates of biomass are of a great importance for studying the dynamics of the fish populations besides the estimates of the population number. The knowledge of values of biomass and recording of the rate of the fish growth make it possible to

determine annual production of the population, often interpreted as a limit of optimum yield, which do not threaten the stability of the population.

It is obvious that the relative stability of the biomass is not dependent only on the recruitment, however, particularly on a varying rate of the weight growth, connected with the abundance of fishes in the reservoir. If we evaluate this stability as significant, it would be necessary to consider the presence of a regulation mechanism in the population providing more or less a stable behaviour of the system in time. On the other hand, it is possible to observe that the dynamics of production exerts a larger variability in comparison with biomass, (Table 5). This character of its changes reflects not only changes of external conditions affecting the rate of the fish growth, but also internal changes in population conditioned particularly by changes in the rate of completing the abundance. So, for example an increase of the production of the roach between 1978 and 1979 resulted from an apparently strong year class born in 1977. Other strong year classes were born in 1971 and 1974 (Table 5).

There is no doubt that determination of the relationship between the biomass, production and yield is of importance even in those cases where fishing is performed not only for obtained a certain amount of fish meat, but also as regulatory measure providing a certain species and age distribution of fish biomass in the course of year, e.g. in drinking water reservoirs.

The mentioned model, in spite of the validity of a given parameters, is however unable to estimate absolute values of a optimum yield, which may be altered from year to year in a connection with changes of the recruitment. It is also necessary to take into consideration the fact that mechanisms of the regulation of population also operate by means of the density dependent mortality (see Backiel, LeCren, 1967). However, this values were not included into the model since there are no particular data.

SUMMARY

1. In the years 1977—1979 estimates of the size of spawning shoals of the roach were carried out in the Kličava reservoir (Central Bohemia, 55ha) using values of the coefficient of exploitation. The estimates were compared with those formerly performed according to Schnabel's method. There was a good agreement between the two types of estimates (Table 1. and 2.). In 1980—1983 only old marks from 1977 to 1979 were recorded and the estimates were performed with the help of the coefficient of exploitation and survival.

2. For age groups 2 to 5, which do not participate completely in spawning, the value of the recruitment was estimated and with the help of it the total population number of these age groups was reconstructed (Table 4.).

3. Dependence of changes of the production and yield on the fishing effort was evaluated by a simple simulation model for the whole period of the existence of one generation, starting from its second year of life. The first variant of the model did not consider a negative effect of the population size of the roach on its growth rate. The yield as well as production were shown to be larger during continuous fishery organized throughout the season as compared with single fishery performed in the short time of spawning.

4. When taking into account the effect of the population number on the growth, then as expected, high values of the production as well as yield were found and, in addition to this for lower and medium values of the fishing mortality ($F = 0.1 - 0.9$), the yield was higher in the case of the single fishery. This should be taken into account for an optimal and economical organisation of the fishery.

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HRABEIELLA PERIGLANDULATA GEN. ET SP. N. (ANNELIDA) — A CURIOUS WORM FROM CZECHOSLOVAKIA

Preliminary study

Václav PIŽL and Josef CHALUPSKÝ jr.

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Abstract. *Hrabeiella periglandulata* gen. et sp. n. (Annelida) from South Bohemia, Czechoslovakia, is described and its morphology and anatomy studied. Major features of the genus are compared with those of *Parergodrilus* and *Stygocapitella*. The systematic position of *Hrabeiella* is discussed.

The worm, differing from the other groups of annelids described up to now, was discovered during faunistical and ecological research of soil-inhabiting oligochaetes in South Bohemia. The contribution gives a description of the new genus and species and brings registered knowledge on morphology, anatomy, localities and ecological notes of the worm. It also points out the possible relations within Annelida and it is our first contribution, which will be devoted to the study of this worm.

Methods. Material was obtained from soil samples extracted by the O' Connor's method (1955). Specimens were examined alive, then fixed and preserved in 4% formaldehyde or fixed in Beauchamp mixture for 15 minutes and preserved in 70% alcohol. One part of the specimens was stained by borax carmine and mounted whole to Canada balsam. Some individuals were mounted into Liquide de Swanne for study of setae. From two specimens embedded into synthetic resin, epon-araldite, were prepared semi-thin sections and stained by toluidine blue. Some specimens were dissected in paraffin blocks and stained by hematoxylin and eosin. Illustrations are based on the study of living worms (A), on series of sections (B) and on total preparations (C, D).

Hrabeiella gen. n.

Diagnosis. Body densely covered by cuticular glands, regularly distributed in transversal rows in separate segments. Setae distally shovel-like, arranged segmentally in four bundles, bundles localized ventrally. Dissepiments missing. Hermaphrodite, male genital glands in VI–VII, female genitalia in XII–XIII.

Type species. *Hrabeiella periglandulata* sp. n. from South Bohemia (Czechoslovakia); monobasic.

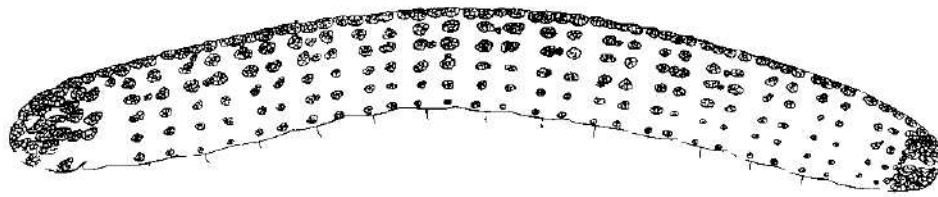
Etymology. The genus is dedicated to Prof. Dr. Sergej Hrabě D. Sc., great Czechoslovak zoologist and specialist in world freshwater Oligochaeta; gender: feminine.

Hrabeiella periglandulata sp. n.

(Figs. 1, 2)

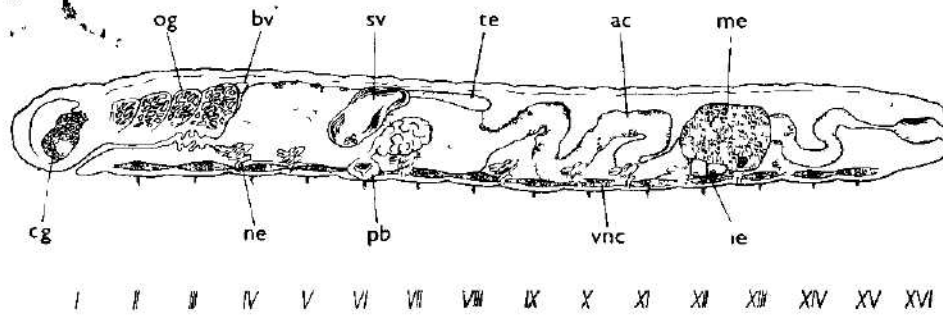
Description. Coloration pale white, body length 1.0–1.5 mm, width 0.10–0.13 mm, number of segments of mature specimens 16 (17 in one case). Body

A

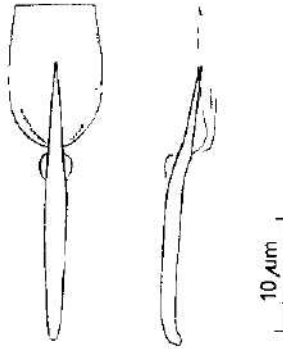


0,5 mm

B



C



D

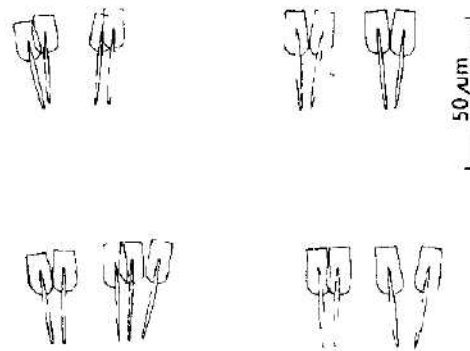


Fig. 1. *Hrabeiella periglandulata* gen. et sp. n.: A — whole specimen, lateral view, B — reconstruction of internal anatomy, ac — alimentary canal, bv — blood vessel, cg — cerebral ganglion, ie — immature eggs, me — mature egg, ne — nephridium,

covered by cuticular glands, finely granulated, coloured olive brown, larger glands oval, smaller of spherical shape (Fig. 1 A). Cuticular glands irregularly and closely applied on head and anal segments, on the other segments in four — complete and incomplete — transversal rows. In complete rows 12 glands. Length of setae 26–39 μm , distally shovel-like broadened (Fig. 1 C). Flattened shovel-like part on its terminal margin 7.5–9.0 μm wide. Whole setae slightly curved, proximally with minute crooked top. Main stem of setae 2 μm thick, nodulus in the middle of the stem immediately below expansion in shovel-like part 3.5 μm wide, lateral margins of shovel-like part slightly bended up. 2 (3) setae per bundle, 4 setae observed in one bundle only. Always 4 bundles per segment, all bundles near to each other on ventral side of body (Fig. 1 D). In the first and last segment of the body setae missing. Head pores and dorsal pores missing. Dissepiments missing. Nervous system formed by head ganglion and simple ventral nerve cord. Alimentary canal: narrow oesophagus with four lobes of oesophageal glands on dorsal side, anterior part of intestine very broad, posterior intestine narrower, sinuous. The intestine expanded into small anal cavity inlaid by dense ciliated epithel in the last segment. Broadened part of alimentary canal irregularly scattered by darker cells, sporadically with oil granula (chloragogen tissue?). Circulatory system: blood colourless, ventral blood vessel along whole intestine, dorsal blood vessel observed closely in front of expansion of anterior intestine, then dorsally only on thin posterior part of intestinal tube. Coelomocytes absent. Nephridia vary, ranging from III–XIII, without interstitial tissue, with complicated twisting efferent duct with apparent atrium, mostly in pairs, sometimes unpaired, missing in some segments. Their absence in genital segments is not a rule. Genital apparatus: clitellum or any cushion of glands around the female pore absent. Spermathecae not observed. Testis in VI, seminal vesicle in VI, sperm funnel and vas deferens not observed. One mature and 1–2 immature eggs in XII–XIII.

Holotypus. No. 1981/1 and 12 paratypes in authors' collection, deposited in the Laboratory of Soil Biology, Institute of Landscape Ecology, České Budějovice
Locus typicus. South Bohemia, district Český Krumlov, Věncová hora near Krnín village, 550 m a. s. l., margin of a meadow on the slope above spruce forest. Soil type: brown meadow soil. 3. 11. 1981, 5 ex.; 5. 7. 1983, 13 ex.; 8. 9. 1983, 1 ex.; 9. 1. 1984, 16 ex.

Further locality: South Bohemia, Bavorov near Vodňany, 445 m a. s. l., soil samples from an apple orchard. Soil type: brown meadow soil. 19. 5. 1982, 2 ex.; 21. 6. 1982, 3 ex.; 26. 7. 1982, 1 ex.

Ecological notes. Worms inconspicuous, minute, after extraction slowly moving. Majority of individuals was obtained from upper layers of the soil, 0–5 cm. Data about bionomy, seasonal dynamics, horizontal and vertical distribution are not known. Feeding habits of the species is also not known, no remains of eaten food were found in the alimentary canal.

Etymology. The species name is derived from the typical cuticular glands covering whole body surface.

og — oesophageal glands, pb — penial bulbs with prostatic glands, sv — seminal vesicle, te — testis, vnc — ventral nerve cord, C — single seta, ventral and lateral view, D — arrangement of setal bundles in two subsequent segments.

Discussion. *Hrabeiella periglandulata* gen. et sp. n. does not seem related to any form in the phylum Annelida. Only two species of the monotypic genera, *Parergodrilus heideri* Reisinger, 1925 and *Stygocapitella subterranea* Knöllner, 1934 seem to resemble the new genus. Controversy about their true position in the system of Annelida went for many years (Reisinger, 1925, 1929, Meyer, 1927, Knöllner, 1934, Karling, 1958) and their systematical position is not satisfactorily resolved up to now, in spite of the existence of the work, which tries to do it (Reisinger, 1960).

P. heideri was described from beechwood soils in Austria and later found in France, Germany and Croatia (in Reisinger, 1960). Reisinger (1925) created a new family Parergodrilidae for his new genus within Archiannelida and after discussions it was transferred into Oligochaeta (fam. Enchytraeidae) by Meyer (1927). Also Černosvitov (1937) cited it in the same way as Meyer did.

S. subterranea was described from interstitial waters of North Sea beaches (Knöllner, 1934) and later found in South Sweden (Karling, 1958). The author of its description placed it to the class Polychaeta (fam. Capitellidae). Karling (1958) established a new family Stygocapitellidae for it and at the same time he pointed out the similarity to *P. heideri*. Reisinger (1960) has compared both genera of these curious worms and came to the conclusion that *Stygocapitella* belongs also to the family Parergodrilidae Reisinger, 1925, which he transferred into the class Polychaeta. Reisinger's main arguments for location these monobasic genera in Polychaeta were following: separate sexes, type of egg-grooving as in Polychaeta and strong similarity of spermatozoa to Polychaeta Sedentaria.

Both species have the same basic plan of structure of the nervous system as *H. periglandulata* as well as the same alimentary canal and probably blood vessel system and lack the septa. Moreover, *S. subterranea* has the same type of anal cavity slightly covered with cilia. Both species differ fundamentally from *H. periglandulata* in the gonochorism, shape of setae and in the missing cuticular glands. *S. subterranea* lives in a quite different environment.

Combination of features postulated in *H. periglandulata* — hermaphrodite, relatively long distance between male and female genital organs in body cavity, missing septa, shape of setae and the arrangement of conspicuous cuticular glands is an entirely unprecedented combination of features which does not allow to place *H. periglandulata* to any known family or order of Oligochaeta.

Considering the approaches to zoological systems of Oligochaeta (Timm, 1981, Brinkhurst, 1982) it may be possible to hold it for a new class of the phylum Annelida. On the other hand, however, the question of possible relation of *Hrabeiella* to the family Parergodrilidae remains to be solved hereafter.

The interpretation of the described facts is extremely difficult, owing to a small number of *H. periglandulata* specimens already examined and it would be untimely. Only further detailed study of internal anatomy, bionomy, ecology and distribution will enable more complete conclusions on its true systematic position and relations in the phylum Annelida.

Acknowledgement

The compendious discussion of many questions concerning the anatomy of the species and its systematic position is gratefully acknowledged of Prof. Dr. Sergej Hrabě D. Sc. For the help and advise concerning the semi-thin sections we are obliged to Dr. František Weyda C. Sc.

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The Figure 2 will be found at the end of this issue.

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RETINAL PROJECTIONS IN CROCIDURA SUAVEOLENS (SORICIDAE, INSECTIVORA, MAMMALIA). THE PRIMARY OPTIC PATHWAY*

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Abstract. Retinofugal projection into primary optic centres in the diencephalon (corpus geniculatum laterale, area prepectalis) and in the mesencephalon (tectum opticum of colliculi rostrales) was examined in 3 ♀♀ and 2 ♂♂ of *Crocidura suaveolens* that had undergone bilateral eye enucleation. Functionally and evolutionally interpreted results are compared with data in literature.

INTRODUCTION

Within the framework of a study of locomotor activity in *Crocidura suaveolens* it was necessary to perform bilateral eye enucleation in order to prove the existence of a free-running rhythm of locomotor activity (Sigmund and Sigmund 1983 a). The function of the optical system in the life of soricids has not yet been fully understood (Grünwald 1969). It is probable that in this group the optic system acts as a synchronizer with the "Zeitgeber".

The pathways and site of terminations of the retinal ganglion cells have been extensively studied in numerous vertebrate species by a variety of methodological approaches (Polyak 1957, Hayhow 1959, Hayhow et al. 1960, 1962, Ebbesson 1970, Rusak and Zucker 1979). According to a generally accepted view the mammalian optic system can be characterized as consisting of three major central projections: 1. primary visual pathway, 2. accessory optic pathways, and 3. retino-hypothalamic projection.

The structure of cortical and subcortical optic centres and the organization of their projections in insectivores have received little attention. Retinal projection and its termination in subcortical structures have been described in hedgehogs of the genera *Erinaceus*, *Paraechinus* and *Hemiechinus* (Campbell et al. 1967, Campbell 1969, Tigges and Tigges 1969, Moor 1973) and in the mole (Lund and Lund 1965, 1966). The structure of subcortical optic centres in soricids has been studied by Campbell and Ryzén (1953), Bauchot (1963), Campbell (1972) and Sato (1977), but retinofugal projections has not yet been investigated.

The object of the present study, some of whose results have already been reported (Sigmund 1983, Sigmund and Sigmund 1983 b), is to check the extent of the primary visual pathway and its terminations in the subcor-

* A joint research project of the Charles University, Praha and Humboldt University, Berlin.

tical diencephalic and mesencephalic structures of *Crocidura suaveolens*. This species, a representative of the most primitive, originally terrestrial insectivores stands at the base of the evolutionary line of placental mammals including primates and hence culminating in man (Stephan 1967).

MATERIAL AND METHODS

Basic data on the number, sex and weight of the experimental animals as well as information on the date of eye enucleation and length of survival period are given in Table 1. The animals were reared in a laboratory under constant light conditions of a LD cycle 12:12 (white light 80:0 lux, L: 0700—1900). The room temperature fluctuated about 20 °C throughout the experiments, at relative humidity of 70—80 %.

Eye enucleations were performed under ether narcosis, using a stereoscopic microscope. The postoperation field was treated with a locally applied antibiotic (Ophtalmoframykoin ung., Spofa). After an appropriate survival period the animals were perfused with a solution of Michaelis buffer (pH 7.4) followed by 4 % neutral formol in Sørensen phosphate buffer (pH 7.4). Their brains were dissected out, blocked and stored in 4 % neutral formol (pH 7.4). Fixation time was eight weeks for animals Nos. 12/82, 13/82 and 14/82, ten weeks for Nos. 15/82 and 16/82.

The blocks were then sectioned 30 µm thick in the coronal plane on a freezing microtome. After a brief rinse in distilled water, the sections were processed by Fink-Heimer staining procedure I (1967). Two series of sections were made of each animal. The sections of one series were pretreated in 0.05 % potassium permanganate for 5 minutes, those of the other series were pretreated in the same solution for 10 minutes.

RESULTS

A. Chronobiological and behavioural findings

All the shrews were significantly synchronized with the 12:12 photoperiod prior to the eye enucleation. The synchronization is a proof of prevalently nocturnal locomotor activity in the species (Fig. 1). A free-running rhythm that could be altered neither by rearing in constant darkness (DD) nor in constant light (LL) (Fig. 1) was established in all five animals already on the day of the bilateral eye enucleation (cf. arrow in Fig. 1). The blind shrews then behaved as intact animals under DD conditions. The eye enucleation proved that the rhythm of locomotor activity is synchronized with the "Zeitgeber" through eyes also in *C. suaveolens*, and the free-running rhythm proved that all rests of photosensitive tissue had been removed by the eye enucleation.

Our experiments have also shown that animals whose eyes have been enucleated easily survive, orientate themselves in the terrarium without apparent difficulties, and feed well. Body weight of the eye-enucleated animals given in Tab. 1, ranging within the average limits for trapped wild shrews, indicates their good condition. The fact that two animals (Nos. 25 and 27) used at the present time for behavioural experiments have been surviving in the laboratory for over a year is another proof of a good physical condition of optically deprived shrews. They find their way through the labyrinth of the experimental apparatus as easily as intact animals (oral communication by Miss Cizová).

B. Neuroanatomical findings

An impregnation method that was used for processing the material enables simultaneous visualization of the antegrade degenerating axons, their preterminal fragments and degenerating axon terminals (boutons terminaux). Similar results were obtained in all animals subjected to bilateral eye enucleation.

Table 1

Animal	Sex	Weight in g	Date of eye enucleation	Survival period in days
12/82	♀ ad	6.2	6 September 1982	9
13/82	♀ ad	7.0	6 September 1982	9
14/82	♀ ad	5.7	6 September 1982	9
15/82	♂ ad	7.4	6 September 1982	10
16/82	♂ ad	6.5	6 September 1982	10

The optic nerves and the optic chiasm are very small, flattened and packed with degenerated axons. Several small bundles of degenerating axons leave the dorsal margin of the optic chiasm and enter the ventral hypothalamus (Fig. 4). Caudad, the optic tract is laterally and dorsally shifted to the surface of the lateral geniculate body (Fig. 2). Preterminal degeneration and degenerating boutons are bilaterally found in the dorsal and ventral subdivisions of the lateral geniculate body (Fig. 5). Similarly as in *Erinaceus europaeus* (Cf. Campbell et al. 1967), more preterminal and terminal degenerations are present in the dorsal subdivision of the lateral geniculate body, where degenerating boutons are present in the peripheral as well as central parts of the body.

In the pretectal area similarly as in the lateral geniculate body, many degenerating axons leave the overlying optic tract and terminate bilaterally (Fig. 6).

A large number of degenerating axons and their terminals was bilaterally found in the stratum zonale and stratum griseum superficiale of the rostral colliculus. Markedly fewer degenerated terminals were found in the stratum opticum and stratum griseum intermedium (Fig. 7).

DISCUSSION

Our behavioural experiments with shrews bilaterally deprived of vision as well as intact have shown that the eye of *C. suaveolens* is an organ enabling synchronization of locomotor activity with photoperiod (Sigmund and Sigmund 1983 a), but its importance for spatial orientation has not yet been proved. Our findings are in keeping with the results of behavioural observations by several authors, which have recently been assessed by Grünwald (1969), Vlasák (1970) and Braniš (1981). Also these authors agree that the function of eyes is negligible, or even without any importance for spatial orientation in soricids. A definitive answer will be obtained only through experiments based on operant conditioning. Only Grünwald conducted such experiments with the object of determining response to light, but their results were not significant. Two of his 5 conditioned individuals of *C. russula* would run to source of light, but the other three did not respond to a 100 or 180° change in its position (Grünwald 1969).

Anatomical findings in the eyes of soricids, summarized by Grün and Schwamberger (1980) and Braniš (1981) are in sharp contrast to the results of ethological observations. These and other authors (referred to by Grün and Schwamberger 1980) share the opinion that the soricid eye

is well developed. Their papers also show that it contains all structures of the eyes of diurnal mammals except for fovea centralis. The presence of both types of receptors, rods and cones, in the retina of shrews is considered sufficiently proven (B r a n i š 1981, on light microscopy level) although the cones in soricids have been defined as only rod-like cones by G r ü n and S c h w a m b e r g e r (1981) on the basis of their study of ultrastructure. Our results on primary optic centres in the brain of *C. suaveolens* are in keeping with the anatomical findings in the soricid eye.

The present results show that the primary visual pathway in the soricids terminates in both subdivisions (ventral and dorsal nucleus) of the lateral geniculate body, in the pretectal area and in the rostral colliculus, similarly as in the other mammals (E b b e s o n 1970, C a m p b e l l 1969, C a m p b e l l et al. 1967). We cannot make any statement concerning differences between the crossed and non-crossed components of retinofugal projection because we used animals both eyes of which had been enucleated. The distribution of preterminal and terminal degeneration in the primary visual pathway of *C. suaveolens* is basically similar to that in hedgehogs, except for projection into the rostral colliculus (C a m p b e l l 1969, C a m p b e l l et al. 1967). C a m p b e l l described quite dense preterminal and terminal degeneration in stratum griseum medium, stratum opticum, stratum griseum superficiale and stratum zonale in the hedgehogs (*Erinaceus europaeus* and *Paraechinus* sp.) after unilateral eye enucleation, using material processed after N a u t a - G y g a x (1954) and F i n k - H e i m e r (1967). The pattern of degeneration in the ipsilateral rostral colliculus was similar but its extent was smaller. In *Crocidura*, we observed dense terminal degeneration in stratum zonale and stratum griseum superficiale, but a smaller amount of terminal fragments was present in stratum opticum and stratum griseum intermedium.

L u n d and L u n d (1965, 1966) described the primary visual pathway in the mole (*Talpa europaea*) after unilateral eye enucleation. They identified pericellular preterminal degeneration stained by the N a u t a - G y g a x method with certainty only in the contralateral pretectal area. A small number of degenerating fibres was regularly found in the ventral part of the contralateral geniculate body. No degenerated axons were found in the ipsilateral and contralateral rostral colliculus of any animal. The different organization of retinofugal projection in the mole may be due to specialization in the subsoil way of life. However, it cannot be excluded that employment of a more subtle method for visualizing the terminal degeneration (Fink-Heimer method) or the use of horseradish peroxidase and tritiate amino acids in tracing retinal projections in the antegrade direction would produce more detailed information on this insectivore.

The visual abilities of shrews can hardly be assessed on the strength of our present knowledge of the subcortical primary optic centres. According to G o u l d et al. (1964), "the region of the brain devoted to vision in the shrew is poorly developed". C l a r k (1932) reported that the "lateral geniculate body in the shrew is small, but its two elements (dorsal and ventral nuclei) are well differentiated". Also S a t o (1977) regards the subcortical primary optic centres in *Sorex chiro* as well-developed; this is in keeping with our findings in *C. suaveolens* and *S. araneus* (Figs. 2 and 3). Quantitative relations in the diencephalon of insectivores were studied by B a u c h o t (1963) who found that the lateral geniculate body of *S. araneus* is smaller by half (index 56) in

relation to body weight than in *C. russula* whose body size is almost the same (index 105). The index is only 29 in *Talpa europaea* whose eyes are greatly reduced. Differences in the size of area pretectalis are not so conspicuous. Values given by Bauchot (1969) indicate that the lateral geniculate body is larger in Crocidurinae than in Soricinae. For the time being it is impossible to say whether the primary state or reduction is the case in Soricinae. Rose (1912), investigating the cytoarchitectonic structure of cerebral cortex in small mammals, found that in *S. araneus* the structure of the area corresponding to visual cortex (area 17) does not much resemble the typical „Calcarinatypus“, but still it is more developed than the same area in *Talpa europaea*. According to Rose, it is reduction in both species.

Another material is under study; it will enable us to evaluate the ipsi – and contralateral components of retinofugal projection in soricids that have undergone unilateral eye enucleation, and to form an opinion of the organization of accessory optic pathways and, perhaps, retino-hypothalamic projection.

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SUMMARY

The distribution of retinofugal fibres was investigated in 5 shrews (*Crocidura suaveolens*) which had undergone bilateral eye enucleation. The material was impregnated after Fink-Heimer (1967). The preterminal and terminal fragments of degenerated axons were bilaterally found in the dorsal and ventral subdivisions of the lateral geniculate body and in the pretectal area. Degeneration prevailed in the superficial layers of the rostral colliculus.

The subcortical primary optic centres of *C. suaveolens* are well developed. Our findings are consistent with those by Clark (1932) in *Sorex araneus*, Campbell and Ryzen (1953) in *S. cinereus*, and by Sato (1977) in *S. shinto*. A discord between the neuroanatomical findings and behavioural observations in shrews, according to which the function of the optic system is poor, must be examined using operant-conditioned animals in exactly defined neuroethological experiments. Only then it will be possible to assess the phyletic level of the optic system in the shrews.

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The figures will be found at the end of this issue.

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**EARLY MORPHOGENESIS OF THE NASAL APPARATUS IN THE LITTLE GREBE
(*PODICEPS RUFICOLLIS*) (AVES)**

Morphogenesis of the Nasal Capsule and the Epithelial Nasal Tube in Sauropsida XII

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Abstract: Unlike most other birds, the little grebe does not develop any vestibular turbinal – atrioturbinal. The author has presumed the cartilage reinforcement of the nasal capsule of the chondrocranium to be a secondary structure evolving in conformity with the requirements of morphogenesis of the epithelial nasal tube, and searches for the causes of absence of this turbinal in early embryos of the species *Podiceps ruficollis* Pallas. He finds out that the virtual cause is due to rather rudimentary development of the vestibule, whose lateral compartment fails to develop, and in consequence no concavity arises, into which normally the atrioturbinal grows as a support of the vestibule. Besides, he ascertains the so-called choanal passage (“Choanengang”) to take here its anlage from two formerly separate elements: dorsally from the ventrally directed diverticulum of the main cavity, and ventrally from the outer choana proper. Later on both these structures fuse.

INTRODUCTION

Our preceding studies of the development of the nasal apparatus in Sauropsida (Slabý, 1979 et seqq.) led us to the conclusion that the cartilage nasal capsule and its derivatives constitute a very plastic covering, which responds most sensitively to the structural changes of the epithelial nasal tube and its appurtenances, and that the particular cartilaginous and osseous structures are to be taken for depending directly upon the functional sensory or respiratory epithelium as well as upon the effect of its induction. Presenting a study of the rostral region of the nasal apparatus of the little grebe we want to introduce an example of mutual interdependence of all these structures. It was namely Toerien (1971) who pointed out that in *Podiceps cristatus* L. no atrioturbinal (vestibular turbinal) develops in the course of morphogenesis, and hence we intend to show on early morphogenesis of the species *Podiceps ruficollis* Pall. why the atrioturbinal does not evolve in this family, whether this reflects any dependence upon the development of the nasal tube, in the given case of the vestibule, whose development in representatives of the class Aves appears just as constant as the development of the atrioturbinal.

MATERIAL AND METHOD

We disposed of two little grebe embryos, 23 and 29 mm in length, for our work. Both the stages were younger than those of which Toerien could avail himself. The embryos were fixed in Bouin's picroformol, embedded in paraffin, cut into 10 μ m sections, and stained with hematoxylin and eosin.

DESCRIPTION OF THE TWO STAGES

Embryo 23 mm in length

In the area where the epithelial solid nostril invaginates, the processus praenasalis, formed now of already fully differentiated cartilage, lengthens dorsally and little by little turns into the cartilage nasal septum (Fig. 1). To its dorsal tip join the paired plates of prochondral tissue furnishing the primordium of the rostral part of the parietotectal cartilage (cupula nasi ant.), which here develops evidently quite separately and independently of the septum. The nostril passes into the anlage of the vestibule, which displays not even in the least any appearance of, or any resemblance to, a primordium of the bird's typical vestibule, such as we saw in other species, but is rather reminiscent of anlage of the vestibule in Lacertilia, to the representatives of which we have devoted our previous studies (Slabý, 1979 et seqq.).

Rostrally, the anlage of the vestibule shows in cross section the shape of a solid short epithelial bar oriented sagittally and having a slight concavity on the lateral side. When proceeding further caudally, this bar dilates more and more ventrally, and into the above lateral concavity protrudes the ventrolateral edge of the parietotectal cartilage spreading here into the area of the condensed mesenchyme, which forms the anlage of the atrioturbinale (Fig. 2). The lateral arm of the vestibule does not yet (and not later on either) develop at this stage. However, in other birds too, e. g. in *Larus ridibundus* as we have shown earlier (Slabý in press, b), it is also the medial arm that takes its anlage as the first one at such early stages of morphogenesis. And this is the reason as well, why the anlage of the atrioturbinale does not possess any outer epithelial wall.

Going on observing still further in an aboral direction the nasal septum, and hence also the whole nasal apparatus, grows higher, the vestibule lengthens and acquires a lumen sending out, about its mid course, a process ventromedially, i. e. in the direction towards the septum. Here the vestibule already passes into the main cavity of the nasal tube. This is arranged so that the most caudal vestiges of the vestibule remain preserved at its originally ventral end, which now begins to turn off and orient itself in a lateral direction so as to produce a small canal forming the anlage of the aulax. The remains of the epithelial vestibule are here to be seen as some ventrally directed epithelial appendages. In this area, the condensed mesenchyme of the anlage of the atrioturbinale dwindles away, nevertheless it remains connected by a narrow bottleneck of its thickened stuff with the somewhat more caudally seated prochondral anlage of the maxilloturbinale.

Also that more rostrally, initially ventromedially oriented arm begins to straighten out into a sagittal direction, and still more caudally it points right ventrally. The aulax extends in a dorsolateral direction so that now both the stem part and the aulax of the main cavity have become well developed. Into the angle between the two penetrates the prochondral tissue of the ventral edge of the parietotectal cartilage, forming here already an extensive anlage of the maxilloturbinale (Fig. 3).

The ventrally directed arm lengthens, luminizes, and fuses with the outer choana (Fig. 4). Both these parts, i. e. the ventrally leading arm of the main cavity and the choana, will keep on individualized as well in subsequent stages, and this ventrally descending arm corresponds to the descending arm of the

choanal passage of reptiles. It links here up with the choana that grows considerably wide dorsally during morphogenesis and would deserve, as we have touched on elsewhere (Slabý in press, d), a new morphological term since it has nothing to do with the "Choanengang" in reptiles, to which in birds the stem part with the aulax correspond.

The epithelium of the above dorsally lengthening choana deflects by its dorsal end a little laterally. Out of this dorsolaterally directed bling process of the choana arises later on a diverticulum corresponding to the Beecker's "Winkeltasche" (side pocket) in reptiles. Into this choanal epithelium here enters, too, the solid anlage of the nasolacrimal duct.

The nasal apparatus has got considerably higher and hence also the stem part as well as the side wall formed by the parietotectal cartilage terminating ventrally with an insert of the maxilloturbinal.

The rostral part of the maxilloturbinal links up with the parietotectal cartilage, which conjoins the septum. However, this connexion is getting loose in a caudal direction, although no sign of an independent anlage of the paranasal cartilage appears. Further caudally, the anlage of the parietotectal cartilage joins itself on to the septum again, yet exhibits everywhere much more inferior tissue differentiation than the septum does, contrasting sharply with it even along the line of commissure so that there can be no doubt about its independent differentiation.

In a caudal direction the maxilloturbinal as well as all the other cartilage capsule evince still more advanced tissue differentiation being formed of young cartilage. Further particulars link up with the description of Toerien (1971), however.

Emryo 29 mm in length

The massive epithelial solid nostril is invaginated from the lateral side and directed ventromedially towards the lower half of the cartilaginous septum nasi (Fig. 5). The parietotectal cartilage links up with the lateral side of the dorsal part of the septum, but there cannot be any doubt that it constitutes here an independent element being separated from the septum and formed of much younger cartilage. In a dorsomedial direction the medial part of the nostril tapers off into a tip that touches the septum and already corresponds to the medial compartment of the vestibule in other birds. Dorsally, this vestibular part exhibits a concavity, into which projects only a very slight vestige of the atrioturbinal. This one is only to be seen in the completely rostral region, being lost a little more caudally. The anlage of the parietotectal cartilage grows considerably wide laterally, while the concavity of the vestibule anlage remains without any mesenchymal support.

In a caudal direction the vestibule loses its prior connection via the nostril with the surface, the nasal septum grows higher, and thereby the medial part of the vestibule lengthens (Fig. 6). The ventral edge of the vestibule has spread almost to the level of the lower edge of the nasal septum. The lateral compartment of the vestibule does not develop at all, only the medial part running somewhat obliquely dorsomedially is formed. Facing ventrally, it is dilating so as to shape a very broad, so far solid epithelial formation showing in cross section an irregular quadrangle. This state fairly conforms with conditions in stages of very early embryos of other birds because not even there is yet the lateral compartment of the vestibule developed.

The dorsal tip of the medial part still touches the septum and, besides, further ventrally, another tip is being formed pointing ventromedially under the basis of the septum (Fig. 7). This tip tapers off caudally into a long process (Fig. 8). Apart from both the mentioned, a further process begins to spring up in the mid length of the medial compartment towards the septum. Continuing in a caudal direction, this process lengthens and runs ventromedially (Fig. 9). Meanwhile, all this tube begins to luminize, the dorsal part of the vestibule is passing quite inconspicuously and without any discernible signs of a transition to the rostradorsal region of the main cavity, and from now on the above ventromedially lengthening process already pertains to the main cavity, too, so that now here remains only a ventrolateral pouchy epithelial formation of the prior vestibule. Facing caudally, that originally rostral and ventromedially directed arm begins to straighten up (Fig. 10), it orients itself into a sagittal direction extending ventrally, so that there arises here a sort of diverticulum of the main cavity leading ventrally and corresponding to the descending arm of the choanal passage in reptiles. It fuses with the outer choana, which is growing considerably wide dorsally (Fig. 11). The most caudal part of the vestibule is only preserved as a kind of ventral epithelial "appendage" at the lateral end of the horizontal passage, forming here the anlage of the aulax.

In a caudal direction the epithelial residue of the vestibule dwindles away and disappears, while the lateral end of the aulax turns off dorsally (Fig. 12). The outer choana has broadened considerably and projects, in a dorsolateral direction, into a long diverticulum, which we consider a homologue of the "Winkeltasche" in reptiles. Here opens then the nasolacrimal duct, at the level of which this diverticulum terminates because its place in a caudal direction is taken by the sacter spreading in this direction still more and more ventrally.

DISCUSSION

In the embryos of birds, the atrioturbinale generally forms a cartilaginous ridge, which springs off the parietotectal cartilage and grows into the concavity of the longitudinal groove of the epithelial vestibule. As we have shown elsewhere, it can either have a simple structure, e. g. in *Larus ridibundus* (Slabý in press, b), or a most complicated one, e. g. in *Corvus*, *Turdus* (Slabý in press, c). In essence, however, the vestibule displays in cross section the shape of a capital U, seeing that it is formed by the medial compartment and the lateral compartment.

In *Podiceps cristatus* L. it was shown by Toerien (1971) that no atrioturbinale would develop at all. Moreover, if we follow morphogenesis of the vestibule (in our case that of *Podiceps ruficollis* Pall.), we find out that also the vestibule, by the induction of which the atrioturbinale develops as its reinforcement, reveals quite different development from that of other birds, as a matter of fact, it is preservation, fixation of the early embryonal stages until more advanced stages and perhaps until the adulthood as well that is the point here. For instance, when we were following morphogenesis of the nasal apparatus in *Larus ridibundus* we saw that in early stages the lateral compartment of the vestibule did not yet develop, so that the ventrolateral edge of the parietotectal cartilage grew into a small lateral concavity of the vestibule anlage, and in this way formed the anlage of the atrioturbinale. Likewise it is also in early

stages of morphogenesis in the little grebe so that even here a vestige of the atrioturbinal appears. Nevertheless, in further stages no lateral part of the vestibule will develop, the parietotectal cartilage will be growing wide by then in a typical way laterally and, except for some hardly perceptible remnants completely rostrally, the anlage of the atrioturbinal will disappear. The vestibule does not go on developing any longer, it remains quite rudimentary, without function, and this is just the reason why the atrioturbinal, in fact the 'vestibular turbinal', does not develop either, this phenomenon being secondary here.

We have also met with the reduction of the vestibule along with the reduction of the atrioturbinal in an advanced embryo of the common pelican (*Pelecanus onocrotalus* L., Slaby (in press, d), where there appears only a slight vestige of the atrioturbinal together with the markedly reduced vestibule, which is rather reminiscent of the vestibule of reptiles. Neither is the atrioturbinal to be found in embryos of the common cormorant (*Phalacrocorax carbo* L., Slaby, 1952) where the vestibule likewise proves considerably simplified (Frankenberger, 1942). At a glance it might seem that the relationships are here primitive. In fact, however, similarly as it comes in the little grebe, the condition here results from the secondary loss of the lateral arm of the vestibule, in consequence of which no dorsal concavity forms and thus no atrioturbinal develops. The high lateral arm of the vestibule (having normally in cross section the shape of a capital U) is that new acquisition of birds and that primary agent which decides whether any atrioturbinal will develop or not. It is here the question of highly specialized relationships, which may in particular come to the fore if we take due account of our theory (in litt.) that the atrioturbinal arises by fusion of the edges of the two capsular elements — cartilago parietotectalis and cart. alaris sup. — and, furthermore, that the atrioturbinal has most probably been preadapted in the common ancestors of reptiles and birds.

It is interesting to note how the rudiment proper of the vestibule continues to proceed in a caudal direction still more and more ventrally, whereas its lengthening dorsomedial process in passing quite inconspicuously to the dorso-rostral region of the stem arm of the main cavity (compare Figures 7–9). The region of this process, dorsally from the outlet of the diverticulum pointing ventromedially and forming the anlage of the descending arm of the choanal passage (i. e., from about Fig. 8 and seqq.), may now be regarded, when observed from a more caudal aspect, as already a component part of the main cavity. In Figures 4, 11, and 12 we can see quite clearly that the structure that has hitherto been named outer choana or choanal passage takes its anlage from two compartments in birds: from the above ventromedial diverticulum running approximately outside the place of fusion of the vestibule and the main cavity, and from the branching off outer choana proper, which is relatively fairly broad and projects laterally into a diverticulum proving homologous with the so-called Beckers (1903) "Winkeltasche" in reptiles.

SUMMARY

The chondrocranium and hence the cartilaginous nasal capsule, too, develops secondarily as a protecting cover of the epithelial nasal tube. The study presented gives evidence of that as well. In the species *Podiceps* it has been ascer-

tained that no atrioturbinal (vestibular turbinal) develops (Toerien, 1971), in spite of its being otherwise a typical structure of the nasal capsule in birds. In our study we have determined the cause of absence of the atrioturbinal to lie in the circumstance that in the little grebe the vestibule develops rudimentarily, especially its lateral compartment fails to evolve, and in consequence no concavity arises, into which normally the atrioturbinal grows as a sort of reinforcement of the vestibule and as a process of the parietotectal cartilage. In a caudal direction, the rudimentary vestibule passes inconspicuously to the stem compartment of the main cavity. Furthermore, it has been found that the so-called choanal passage ("Choanegang") in *Podiceps* takes its anlage from two formerly separate elements: dorsally from the ventrally directed diverticulum of the main cavity, and ventrally from the outer choana proper, leading dorsally out of the oral cavity.

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The figures will be found at the end of this issue.

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ON THE PATTERN OF CORRELATION BETWEEN FISH FECUNDITY AND THEIR LENGTH AND AGE

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To Asst. Professor Ota Oliva, PhD, to whom I am grateful for his continuous guidance and advise

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Abstract. The explanation of some of the reasons for the considerable variety of correlation patterns of fish fecundity and their length and age has been attempted in various populations and species. The existence of a general regularity of fish fecundity growth depending on their length and age is suggested and the pattern of this correlation is discussed

The correlation between the absolute fish fecundity (F) and their length (L) and age (t) has been extensively studied. The pattern and significance of the fecundity-weight (G) correlation were discussed already (Živkov, 1983). As it is known, considerable variations of the F-L and the F-t correlations are described by different equations in different populations and species. The aim of this study was to find the common features of all patterns and the reasons for such a variety.

The final aim is to establish the general regularity of the fecundity growth rate as affected by the length and age.

MATERIAL AND METHODS

The Batak reservoir populations of the goldfish (*Carassius auratus gibelio*), the chub (*Leuciscus cephalus*), the roach (*Rutilus rutilus*) and the bleak (*Alburnus alburnus*) were studied (see details in Živkov, Petrova, 1983) and additional information on populations and species from other reservoirs was obtained from literature references. The correlation-regression analysis was carried out by standard methods (Lakin, 1980). The most adequate equations describing the correlations were selected by mathematical criterions using the following procedure: The parameters of all functions matching the configuration and pattern of the empirically established F-L and F-t correlations were computed. Then the variance $D = (F_i - \bar{F}_x)^2$ of each function was determined, i. e. the summation of the squared differences between the empirical (F_i) and the theoretical (\bar{F}_x) values of the variable (F) were computed. We assumed that the function with the smallest variance would fit best the regularities of variation of the meristics studied (Sepetlieva, 1968).

The asymptotic value A of the logistic function was determined by the graphical method of Walford (1946) normally used to describe animal growth and here used to determine the highest average chub fecundity.

RESULTS

High correlations between average fecundity and the body length values of the Batak reservoir chub, goldfish and roach populations were established. The correlations are almost functional as the correlation coefficients (r) are

close to 1 and are highly significant. Here are the statistics: the chub (Fig. 1, 2) $r=0.986$, Student's $t_{F/L} = 16.8 > t_{\text{tabl}} = 5.04$, $P = 0.001$; the goldfish (Fig 1, 1) $r = 0.969$, $t_{F/L} = 11.77 > t_{\text{tabl}} = 4.78$, $P = 0.001$; the roach (Fig. 2, 2) $r = 0.875$, $t_{F/L} = 4.79 > t_{\text{tabl}} = 3.5$, $P=0.01$.

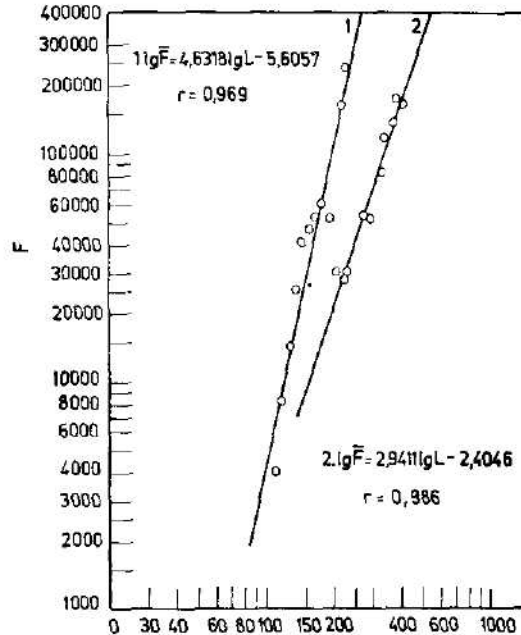


Fig. 1. Logarithmic anamorphosis of the regression lines of the body length (L, mm) and absolute fecundity (F, eggs) of the goldfish (1) and the chub (2) from the Batak reservoir.

No correlation was found in the bleak population ($r = 0.067$, $t_{F/L} = 0.21 > t_{\text{tabl}} = 2.23$, $P = 0.05$) (see Živkov and Petrova, 1983, Tab. 5).

The regression analysis of empirical data showed that the F-L correlations of the former three populations could be described by both the power ($F = aL^n$ or $\lg F = \lg a + n \lg L$) and the exponential ($F = ab^L$ or $\lg F = a + bL$) equations meaning that both the log ($\lg F - \lg L$) and the semilog ($\lg F - L$) regression lines were straight (Fig. 2). As these lines were too similar (Fig. 8 A) the selection of the more adequate one could be done by calculating the variances $D = \sum(F_i - \bar{F}_i)^2$. This showed that the power equation ($\lg F = 2.9411 \lg L - 2.4056$, $\sigma_{F/L} = 9062$) gave a better description of the chub F-L correlation compared to the exponential one ($\lg F = 3.5280 + 0.0044L$) as the variance of the former (8.1×10^5) is smaller than that of the latter (15.3×10^6). In the case of the goldfish the variance of the equation $\lg F = 4.6318 \lg L - 5.6057$, $\sigma_{F/L} = 16137$ is 28.7×10^8 and of the equation $\lg F = 0.0122L + 2.5959$ it is 31.2×10^8 (Fig. 1). In the case of the roach the exponential equation ($\lg F = 0.0105L + 2.71905$, $\sigma_{F/L} = 5344$) gives a better description of the F-L correla-

tion as the variance (3.27×10^6) of the power equation ($\lg \bar{F} = 2.8235 \lg L - 1.9696$) is larger than of the exponential one (2.57×10^8) (Fig. 2).

The F-t correlations of the Batak populations were similar. Here are the statistics: the goldfish $r = 0.97$, $t_{F/t} = 7.438 > t_{\text{tabl.}} = 5.84$, $P = 0.01$; the chub $r = 0.977$, $t_{F/t} = 10.31 > t_{\text{tabl.}} = 8.86$, $P = 0.001$. The F-t correlation coefficient

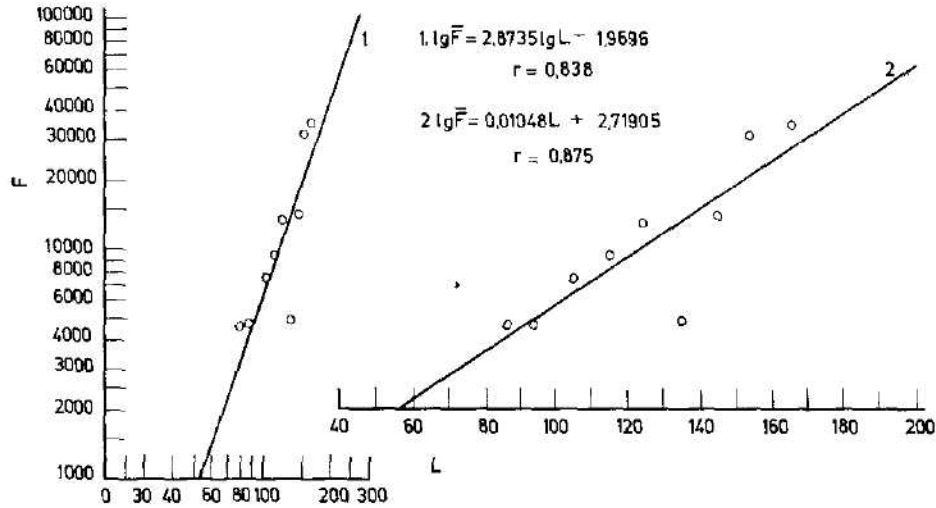


Fig. 2. The correlation between the average body length (L, mm) and the absolute fecundity (F, eggs) of the roach in log (1) and semilog (2) scale.

of the roach is high (0.840) but insignificant because of limited number of age groups ($t_{F/t} = 2.68 < t_{\text{tabl.}} = 3.18$, $P = 0.005$). The bleak showed no F-t correlation because of limited number of age groups and mostly because of irregular fluctuations of F in the available age groups (Živkov and Petrova, 1983, Table 2). This is similar to the low correlation between F and L as well as fecundity and weight (Živkov, 1983). Mackey and Mann (1969) also established low F-L and F-t correlations ($r = 0.2551$ and 0.5312 , respectively) of this species. We suppose that these low correlations occur in species with short life cycles. The Batak bleak population matures very early (at the end of the second year, Živkov, 1980) and for this reason aging occurs in lower age groups.

The F-t correlation patterns show a wider variety compared to the F-L and F-G ones. The power equation ($\lg F = 3.6605 + 1.9179 \lg t$, $\sigma_{F/t} = 4524$, $D = 19.9 \times 10^8$, Fig. 3) gives a better description of the goldfish F-t correlation than the exponential one ($\lg F = 3.7530 + 0.2861 t$, $D = 91.9 \times 10^8$) while in the case of the roach it is the opposite ($\lg F = 3.0984 + 1.7196 \lg t$ with $D = 2.63 \times 10^8$ and $\lg \bar{F} = 3.2345 + 0.21215 t$, $\sigma_{\bar{F}/t} = 3.936$ with $D = 1.38 \times 10^8$) (Fig. 4). The distribution of empirical dots on Fig. 5 exhibiting the chub F-t correlation shows that even three functions are fitting well:

$$\text{logistic} - \bar{F} = \frac{190000}{1 + 10^{1.0914 - 0.2517t}}, D = 7.32 \times 10^8, \sigma_{F/t} = 2163 \text{ (Fig. 5);}$$

logarithmic - $\bar{F} = 262823.771gt - 69806$, $D = 8.54 \times 10^8$ (Fig. 6, Fig. 8, B);
 parabolic - $\bar{F} = -30233 + 3260.753t - 963,017t^2$, $D = 14.55 \times 10^8$.
 The variance of the logistic function is the smallest. The asymptotic value
 $A = 190\ 000$ eggs of the logistic function was determined by the Walford
 graphic method (Fig. 7).

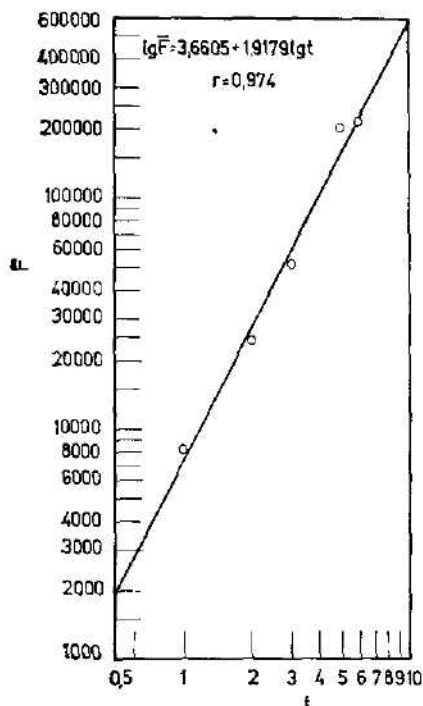


Fig. 3. The logarithmic anamorphosis of the age (t, years) and the average absolute fecundity (F, eggs) of the goldfish.

DISCUSSION

There are contradictory concepts on the regularity of the F-L correlation. This correlation most often is (or is supposed to be) described by the power equation (Bagenal, 1968, Ivankov and Andreev, 1969, Brylinska, 1971, De Silva, 1973, Mann, 1973, 1976, Pither and Macdonald, 1973, Cadwallader, 1976). Others have found that the empirical F-L regression line is close to the power or exponential equation (Bastl, 1961, 1970). Bagenal (1968), Lusk (1968), Kirka (1969), Volskis and Kaminskene (1976) found a linear while Derzavin (1922), Johansen (1955), Volodina (1963), Ivankov and Andreev (1969) found a logistic F-L correlation.

The F-t correlation is most often found or expected to be linear (Bagenal, 1968, Bastl, 1970, Brylinska, 1971, De Silva, 1973, Volskis and Kaminskene, 1976) while Mackay and Mann (1969) used exponential equations for the roach and the bleak. Power or exponential equations were used for the F-t correlations of some species in Soviet reservoirs (Volo-

din, 1963, Turanova, 1972, Trjapicina, 1975). Trjapicina (1975) showed that the empirical F-t regression line of the redeye (*Scardinius erythrophthalmus*) from the Volga river delta is a logistic one.

Both our as well as other authors' results show the wide variety of F-L and F-t correlation patterns.

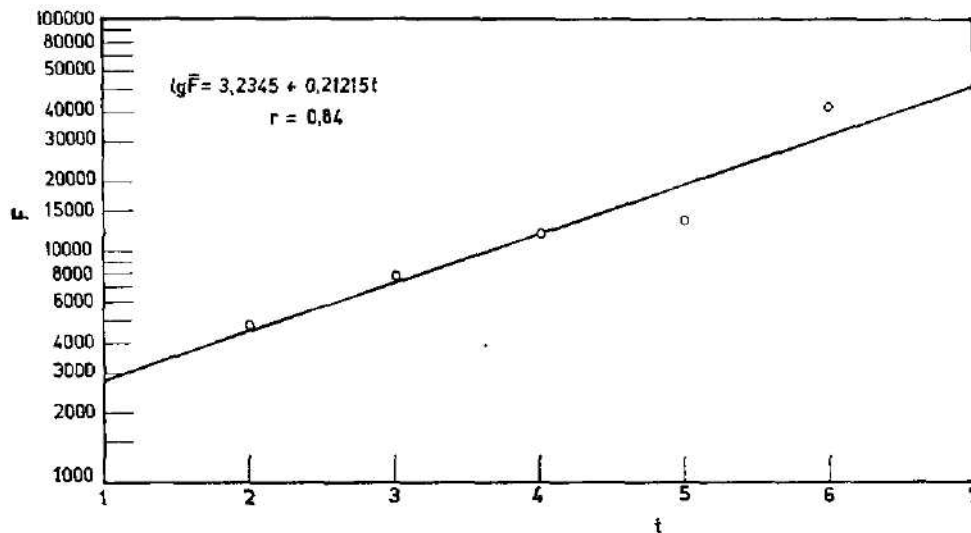


Fig. 4. The correlation between the roach's age (t, years) and average absolute fecundity (F, eggs) in semilog scale.

The problem of the reasons and the very existence of such a variety is a complex one and is to be analysed from various viewpoints. Our biological and statistical analyses showed that physiology as well as timing of maturation, duration of life cycle, age structure of females, samples' representativeness, accuracy of statistical methods affected the functions' patterns.

In various cases the following opportunities exist:

(i) In early maturing populations with no individuals from the highest age and size groups or in samples without such individuals the growth of fecundity as affected by age and size is best described by the power or the related exponential equation (Fig. 8 A the continuous line, Fig. 1-4). A more accurate mathematical analysis of the empirical data may reveal an exponential F-t correlation (as the F-L one) in a much larger number of cases than the ones known so far.

(ii) In later maturing populations or in samples with no individuals from lower age groups and sufficient number of individuals from the highest age groups the correlation is best described by the logarithmic equation (the continuous line in Fig. 8 B and Fig. 6). In this case the authenticity of our assumption on the unified character of the F-t correlation is shown because the chub fecundity growth as affected by age is described equally well by both the log (Fig. 6) and the logistic (Fig. 5) equations.

(iii) In later maturing populations and in samples with insufficient number of high age groups individuals (because of their intensive elimination or nonrepresentativeness of the sample) and no individuals of the lowest age groups, the F-L and F-t correlations can be exhibited by a straight line (Fig. 8 C, the continuous line). This is the most common phenomenon as most investigators

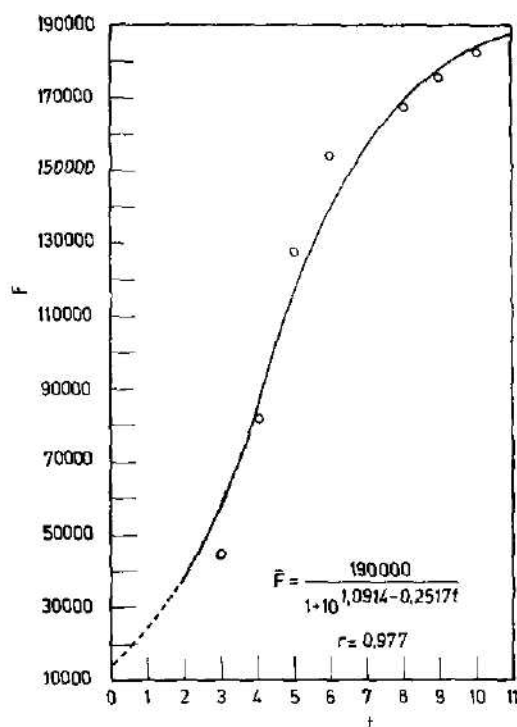


Fig. 5. The correlation between the chub's age (t, years) and average absolute fecundity (F, eggs).

get their materials from commercial catches in which for known reasons individuals of the lowest and highest age and size groups are either missing or rare.

(iv) Populations and species with early maturing and long life cycles and with individuals of all age and size groups available, the F-L and F-t correlations are expected to be of the logistic pattern (Fig. 8 D, Fig. 5).

The analysis of the factors affecting the F-L and F-t correlations indicates that various regression lines of various populations can be viewed as fragments (Fig. 8 A, B, C, the continuous lines) of one common curve — the logistic one (Fig. 8 D). Generally the fecundity growth as affected by the length and age growths follows the logistic curve pattern with the power, exponential, linear and log equations being special cases.

CONCLUSIONS

The correlation between the absolute fecundity (F) of fish of various populations, species and reservoirs and their length (L) and age (t) can be described

by various equations: power (Fig. 8 A, the continuous line or Fig. 1 and Fig. 3), exponential (Fig. 8 A, the continuous line or Fig. 2, 2 and Fig. 4), log (Fig. 8 B, the continuous line or Fig. 6), linear (Fig. 8 C the continuous line) and logistic (Fig. 8 D and Fig. 5). The correlation pattern is determined not only by physiological factors but largely by the timing of maturation, duration of

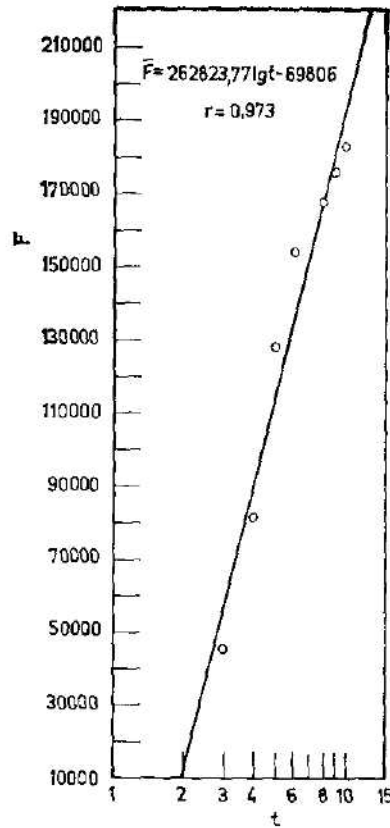


Fig. 6. The correlation between the chub's age (t, years) and average absolute fecundity (F, eggs) in semilog scale.

life cycle, age structure of females, samples' representativeness and accuracy of statistical methods. If all these factors are taken into consideration when studying each particular species and population the seemingly wide variety of F-L and F-t correlation patterns are found to be following the logistic function (Fig. 8 D) and the power, exponential, linear and log functions (continuous lines in Fig. 8 A, B, C, respectively) can be viewed as special cases. In early maturing populations with long life cycles and with sufficient number of individuals of all age and size groups available, the absolute fecundity in the lowest age and size groups is expected to grow relatively slowly (Fig. 8 D), in higher ones — much faster, and almost exponentially. In the highest groups

the fecundity growth will be retarded with the F values approaching an asymptotic average value A (Fig. 5 and 7).

The F - L and F - t correlations of the Batak fish populations were very high, almost functional.

The bleak F - L , F - t and F - G correlations were low and/or insignificant probably because of the bleak's short life cycle.

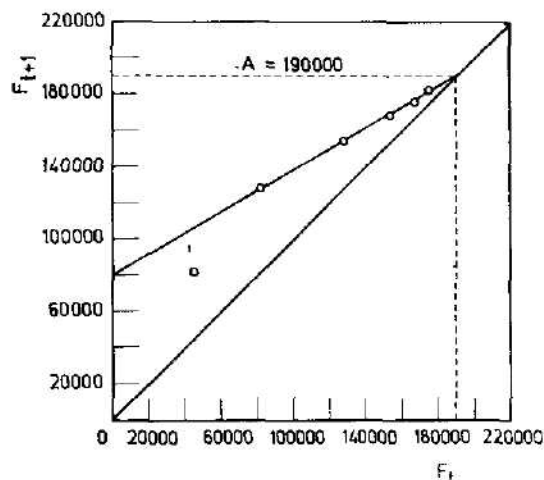


Fig. 7. Walford's regression line between the ohub's absolute fecundity (F) at the age of t years (F_t , eggs) and the fecundity at the age of $t+1$ years (F_{t+1} , eggs). A — the asymptotic average value of the absolute chub's fecundity in the reservoir studied.

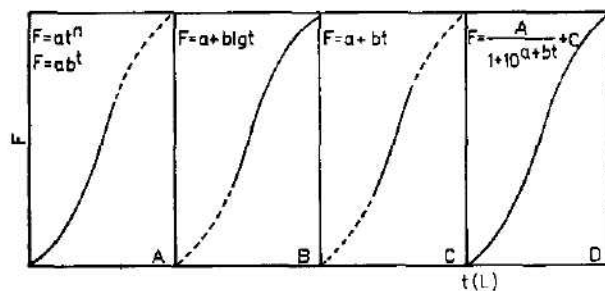


Fig. 8. Patterns of correlation between age (t) or length (L) and absolute fecundity (F) of various populations and species of various reservoirs. The continuous lines show the actually established correlation patterns between t (L) and F : A — power and exponential functions, B — logarithmic function, C — linear function, D — logistic function. The dotted lines show the expected changes of F as affected by t (L).

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Final Report

of the Proceedings of the Meeting of Scientists "Science between War and Peace" which took place on June 24 and 25, 1983, in the framework of the World Assembly for Peace and Life against Nuclear War

The meeting of the scientists came to the following conclusions

1 The participating scientists from the most varied branches of science of 49 countries and partisans of different political opinions and religious beliefs declare that it is the most important task of scientists all over the world to join forces and prevent the use of weapons of mass destruction — the final catastrophe of the whole human civilization — and to participate in the peace camping for nuclear freeze and UN world disarmament campaign

2. A new extreme danger of outbreak of a nuclear war could be created by the planned installation of a new generation of American medium range missiles, extremely through a possible failure of electronic systems

3 It has been proved by the most varied branches of science that nuclear war would mean, in its unavoidable consequences, the end of humanity, the end of nature, the end of all life on this planet — Therefore, the scientists consider the militarist idea, that one of the parties could emerge victorious from a nuclear war, entirely erroneous They consider it equally erroneous and absurd to believe in the possibility of a limited nuclear war — Therefore, they appeal to the Governments of the countries owning nuclear weapons to respect scientific conclusions about the threat to mankind by nuclear war and to do everything to ensure that nuclear energy be used only for peaceful purposes, for the welfare of humanity They declare that the real role of science and scientist is to construct and not to destroy

4 They recommend the Governments of states to increase the role of International Law and accede to the resolution of the UNO General Assembly declaring that the state which would be the first to use nuclear weapons in "preventive", or "defensive" actions would commit the gravest crime against humanity, which could not be justified by any means They recommended all the governments to accede to the international treaties prohibiting chemical and bacteriological weapons and to reduce the enormous mortal stocks of military chemicals

5 They point out that the new phase of development in armaments with its growth of the military industrial complex and the role of militarism in the national and foreign policies increases the mistrust among nations, particularly between the states with different social systems, and threatens international stability They appeal to the highest representatives Governments and Parliaments of the states owning nuclear weapons to reduce the danger of the origin of the nuclear conflict by international negotiations for the limitation of nuclear armaments and gradual disarmament on the basis of the principle of equal security In particular, the plans for new strategic nuclear weapons in Western Europe are creating such universal danger as has not existed ever before

6 They consider the struggle for peace and peaceful coexistence of the states with different social systems to be the most urgent global problem of mankind The arms race drains away enormous economic values and human efforts, thus postponing definitely the possibility for a solution of these problems arising

for mankind and having utmost urgency of the behalf of the Third World. Only in peace is it possible to solve other urgent global problems, such as mass poverty, illiteracy, and disease, preservation of healthy environment for mutually interrelated forms of life on Earth, ensuring food and the necessary resources for mankind and the solution of problems connected with the cultural, economic, scientific and technological development of society. The struggle for peace is closely connected with the struggle for democracy and human rights. In this respect the right of the individual, nations and states to live in peace must be considered the most outstanding fundamental human right.

The struggle for peace is also closely connected with the struggle for social progress, economic and social requirements of the working people of the whole world, and the struggle for the right of development and the new international economic order, as well as the struggle for national liberation.

7. Therefore, they recommend that the partisans of the most varied concepts and theories of peace concentrate fully their attention on what connects the partisans of peace the world over — the endeavour to avert the danger of nuclear war and as a priority measure immediately freeze all nuclear armaments as a step to achievement of general disarmament.

8. They propose the organization of a World Congress of Scientists against War and Armament.

9. They propose the creation of national Committees of Scientists for Peace, which will fight together with natural and social scientists against war.

10. They appeal to the moral responsibility of all scientists of the world to engage in the struggle for peace and against the danger of nuclear war, the responsibility arising from the relation of the scientist to life and mankind, and request them to guide and educate also the coming young generation of scientists to this responsibility. Scientists can make valuable contributions to making people understand better the hazard and the potential consequences of the arms race, particularly its nuclear part.

11. They consider it of vital importance to develop wide international cooperation in investigations necessary to secure peace and prevent the outbreak of a nuclear war. They recommend that UNESCO and all international scientific associations of the most varied branches of science put on the agenda of their world congresses, symposia and conferences — if they have not yet done so — the research of the problem, by the solution of which science could contribute to the development of peaceful coexistence.

12. They address their urgent appeal to the scientists all over the world to work actively in their countries and on international level in favour of the détente, peaceful coexistence of states with different social systems, against the threat of nuclear war and for the protection of life wherever and whenever it may be threatened.

H. D. Gruner (ed.) *Lehrbuch der speziellen Zoologie. Band 1. Wirbellose Tiere. 1. Teil: Einführung, Protozoa, Placozoa, Porifera.* VEB Gustav Fischer Verlag Jena, 1980, 318 stran, 16,50 M

Celé generace evropských zoologů získávaly základní znalosti o oboru z německých učebnic, které měly většinou vynikající úroveň a originální pojetí. Připomeňme při této příležitosti především učebnice Boase, Hertwiga, Stempella a konečně klasické dílo Claus-Grobbe-Kühna. Po druhé světové válce navázal na tuto poslední knihu Kaestner, kterému se podařilo obsáhnout v obdivuhodné šíři řadu nových poznatků a vydat obsáhlé učebnicové kompendium, které se dočkalo několika reedic. Jedenáct let, které uplynuly od posledního, třetího vydání, na němž se ještě plně podílel jako autor, přineslo řadu nových poznatků a názorů na klasifikaci a fylogenezu živočichů v takové šíři, kterou nemůže vyváženě sledovat jediný pracovník. Proto byl vytvořen kolektiv vedený H. D. Grunerem, který by měl v poměrně krátké době vydat mnohohodlnou učebnici, zachycující současný stav poznatků o živočišné říši a názorů na její klasifikaci.

Prvý díl slibuje, že dostaneme do rukou dílo, z něhož budou moci čerpat zoologové i biologové nejrůznějšího zaměření.

Oproti Kaestnerově učebnici byl nově pojat a rozšířen především úvod, v němž jsou shrnuty v pregnantní formě, s velkým přehledem a velice vyváženě postupy zoologické klasifikace. Po krátké definici základních pojmů, včetně vymezení obsahu speciální zoologie je podán krátký přehled vývoje systematiky. Stručně je uvedena rovněž metodika systematické práce, zásady nomenklatury a jsou charakterizovány klasifikační jednotky. Velmi důležitou část tvoří pátá kapitola o metodách systematiky, v níž jsou vysvětlena kritéria homologie a diskutovány i metody fylogenetické systematiky a klasifikace. Šestá část je pouze krátkým uvedením k některým otázkám evoluce. Ze sedmé kapitoly věnované postavení živočichů v říši živých organismů je velmi důležitá část o vzniku mnohobuněčnosti, opírající se většinou o práce západních autorů.

Po těchto prvých úvodních částech následuje na vynikající úrovni a s velkým přehledem sestavené osvětlení vzniku a vývoje stavebních typů a organizace živočichů od rozmnožování přes ontogenezi s důkladným výčtem názorů na vznik zárodečných listů až k larválním stádiím.

Vyvrcholením celého úvodu pak je závěrečná kapitola o vlastním třídění živočichů podaná jako přehled možností různých klasifikací, při nichž autor uvádí i názory na vznik coelomu, jeho redukci a článkování. Diskutuje i problémy prvoretých a druhoretých živočichů, tzv. archicoelomat a to i s historickými odkazy na vývoj názorů na tyto otázky.

Podříši a jediný kmen prvoků zpracoval známý protozoolog Grell s přehledem, opírajícím se o dokonalou znalost látky a zkušenosti získané z vlastní monografie o prvocích. Používá zatím ještě klasický systém rozdělení na 5 tříd a ani nediskutuje některé odlišné názory na klasifikaci prvoků navržené komitétem pro systematiku a evoluci Protozoologické společnosti, která podala poněkud odlišné třídění.

Tento autor zpracoval pak jako přední odborník i skupinu Placozoa. Houbám (Porifera) je věnováno více než 130 stran textu (autor Kilian).

Klasifikace je u prvoků provedena až na úroveň řádů, příp. podřádů s uvedením zástupců, u hub na úroveň čeledí.

Probírání jednotlivých kmenů v tomto díle se opírá o jednotné schéma, které umožňuje rychlou orientaci.

Knih je zakončena obsáhlým přehledem základní literatury rozděleným podle jednotlivých kapitol nebo skupin kapitol. Je uváděna většinou literatura anglosaská, příp. francouzská, ruská, pokud vyšla v překladech.

Poněvadž v textové části jsou uváděni živočichové pouze názvem rodovým a druhovým, je za literaturou zařazen i rejstřík taxonů s uvedením plného označení včetně jména autora popisu a vročení.

Knih je bohatě ilustrována kvalitními jednotně překreslovanými obrázky, často upravovanými a pěti tabulemi fotografií. Pouze u kmene Placozoa postrádáme celkový habitus živočicha. Ten je ovšem znám pouze u jednou nalezeného druhu *Treptoplax reptans*, zatímco všechna novější data se týkají jen druhu *Trichoplax adhaerens*.

Prvý díl tohoto učebnicového kompendia je tvůrčím počinem na vysoké odborné úrovni, podávající současný stav poznatků o živočišných organizmech. Zvláště nutno ocenit přehled základních teoretických přístupů ke klasifikaci, který shrnul vydavatel v úvodu a který by měl znát každý zoolog, nebo biolog. Kniha je psána s vysokou mírou kritického hodnocení všech známých faktů a velmi správně vede čtenáře k tomu, aby nechápal dosavadní klasifikaci živočichů za ukončenou a neměnnou část biologie. Pro tyto klady se stane připravované kompendium důležitým zdrojem poučení pro všechny, kteří se z jakýchkoliv přístupů zabývají živočišnými organizmy.

M. Kunst

Wehner, R., Harkness, R. D., Schmid-Hempel, P.: *Foraging Strategies in Individually Foraging Ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae)*. 79 pp., 29 figs., 2 plates, 2 maps. G. Fischer Verlag, Stuttgart & New York, 1983. Price DM 34.00 (paperback).

In contrast to the laboratory neurophysiological or cybernetic approach to orientation behaviour, this is a complex field study of foraging behaviour of an interesting desert ant. While studying the ant in its natural environment the authors ascertained all essential ethological and ecological parameters of foraging. The species seems to have been well chosen for this purpose. It is a solitary diurnal forager and individual ants, large and conspicuous, are easy to observe and can be labelled with coloured tags.

Two separate populations of *C. bicolor*, living about 1250 km apart in northern Greece and in central Tunisia, were compared. The two regions differ in weather conditions; food is more abundant and, consequently, the population density of the ant is higher in Greece owing to about five times higher annual rainfall. These differences affect some parameters of the foraging behaviour: in Greece, the foraging range of a colony is smaller, foraging runs are much shorter, and also the foragers themselves are substantially smaller. The life expectancy of the foragers is 6 days at both sites; about 50 % of them return with prey, and the overall intake of solid food is nearly the same. Particularly interesting is the finding that all foraging trips of an individual ant are restricted to a part of a circular foraging area measuring 30–40 m in radial length and only 50–60°. The authors give an astute explanation why the foraging range is so strictly partitioned among individual ants: owing to high environmental pressure (food, predators) their walking speed is high and navigation strategy apparently very efficient.

Congratulations to the authors on their achievement; the combination of the field ethological and ecological approaches and the comparison of two geographically distant populations will very probably make this concisely written study a citation classic.

I. Hodek

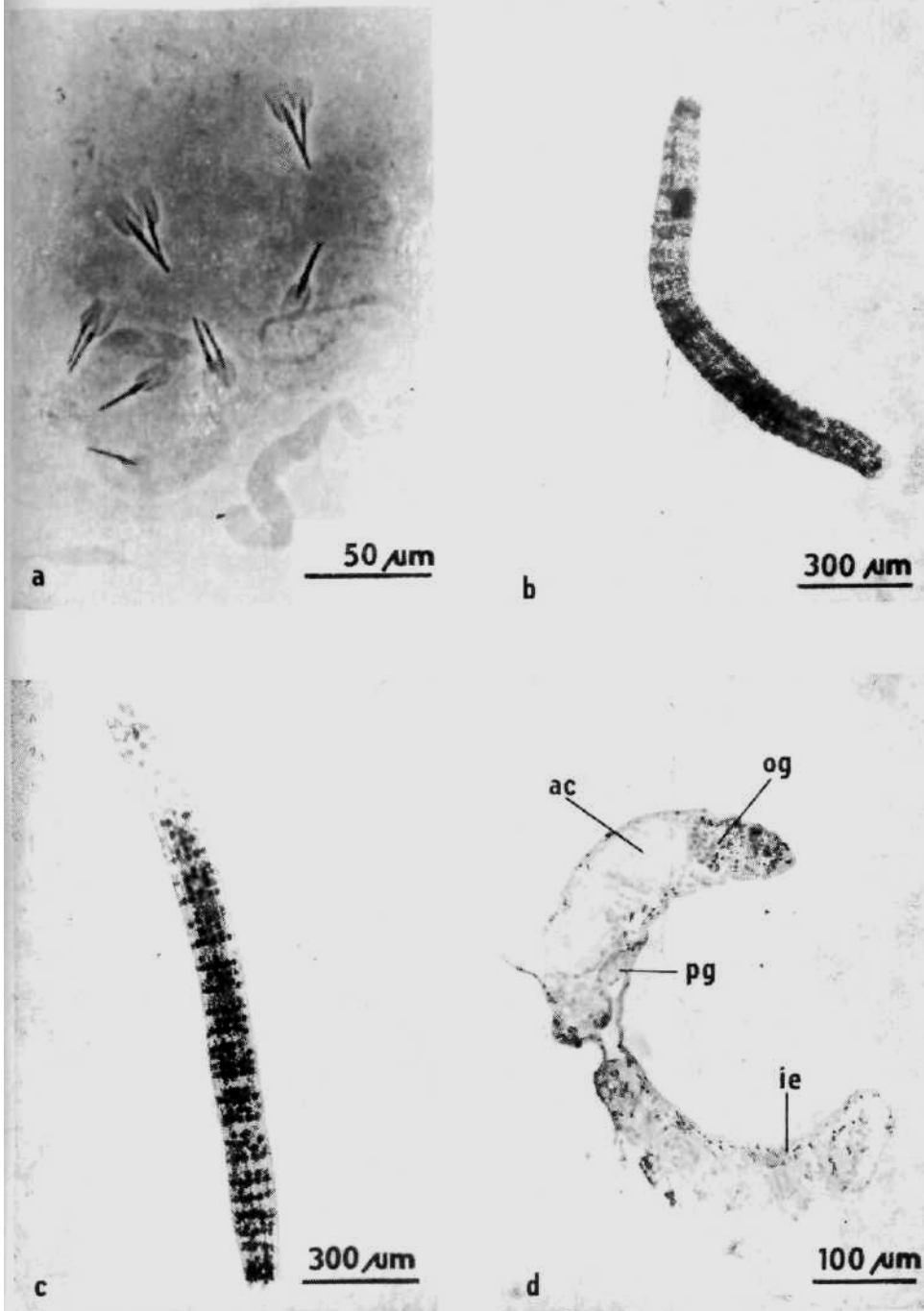
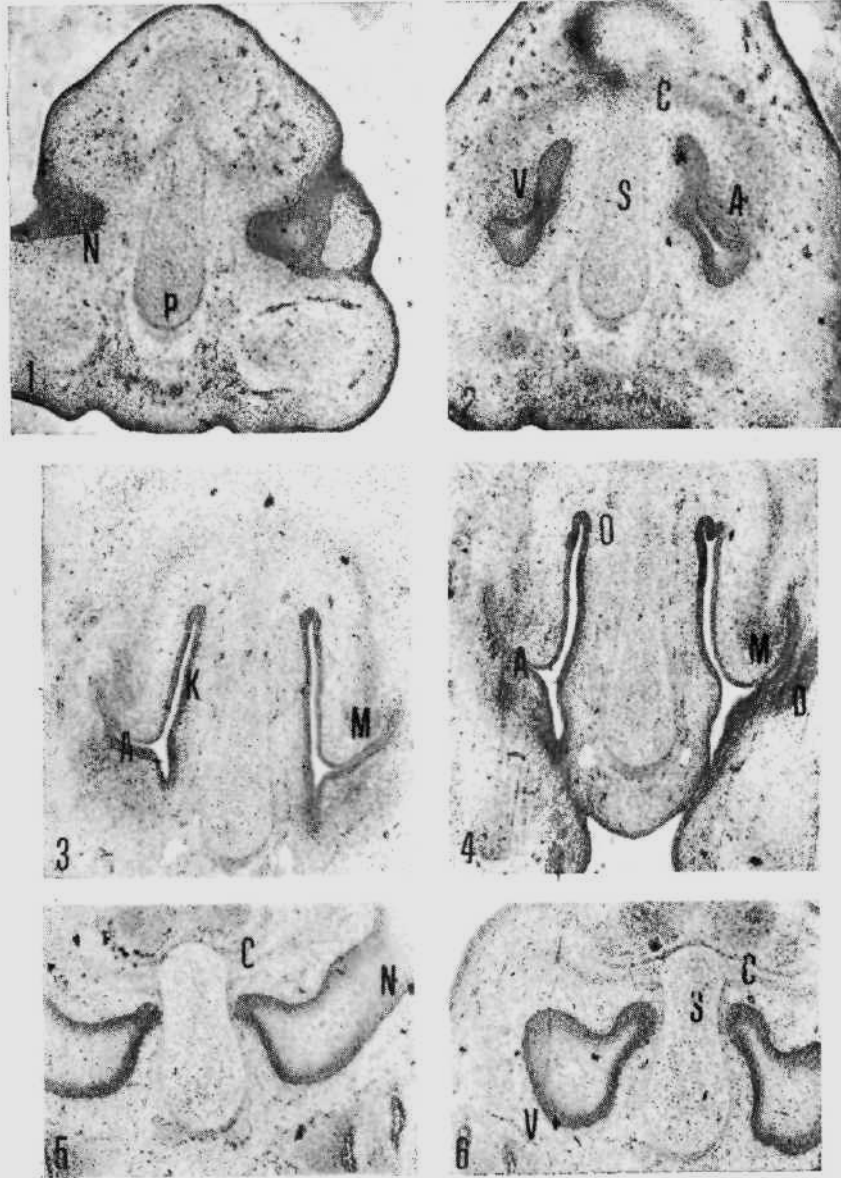
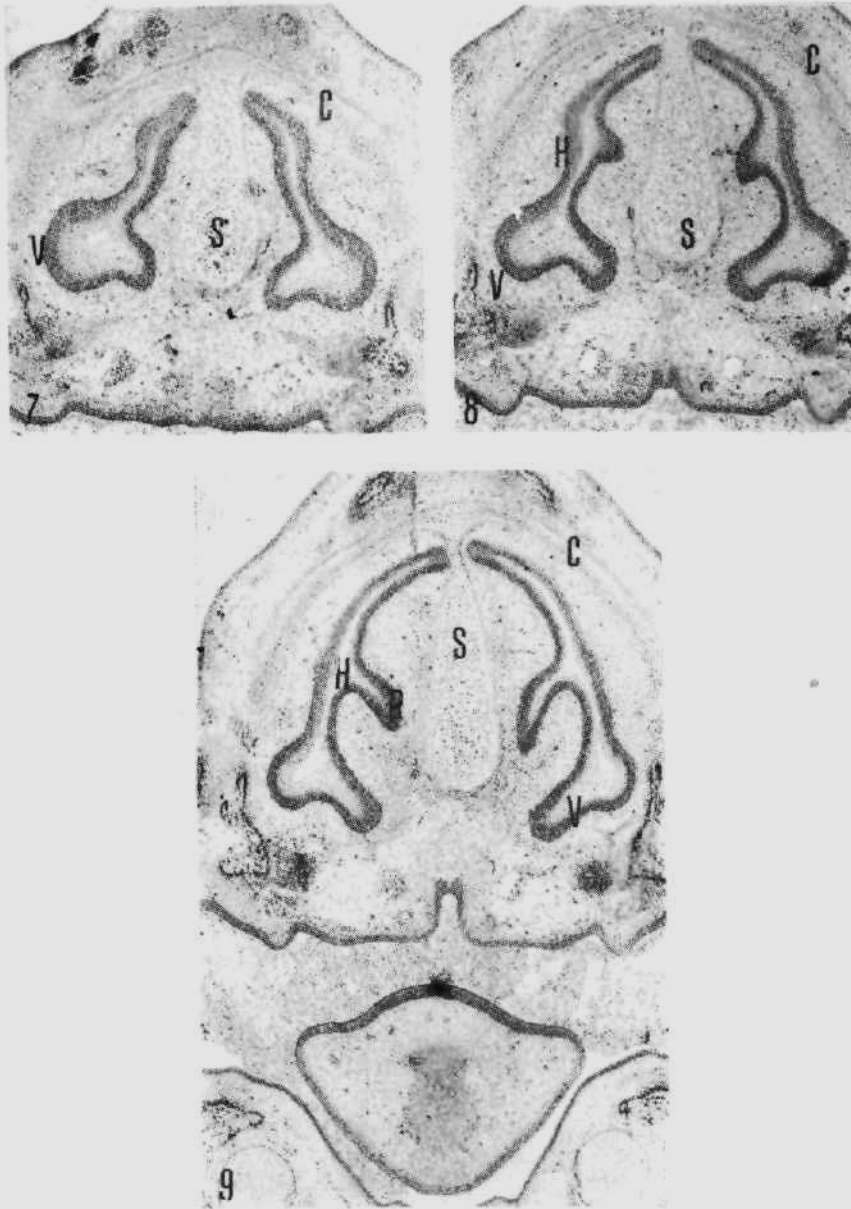


Fig. 2. *Hrabeiella periglandulata* gen. et sp. n.: a – setae in phase contrast, b, c – specimen alive, d – longitudinal paraffin section, ac – alimentary canal, ie – immature eggs, og – oesophageal glands, pg – prostatic gland.



Figs. 1-4: Sequence of cross sections of anlage of nasal apparatus of 23 mm *Podiceps ruficollis* embryo, in rostrocaudal direction. 1 - section of region of entrance to nostril, 2 - section of region of vestibule, 3 - section of mid region of nasal apparatus, 4 - section of caudal region of nasal apparatus. Figs. 5-12: Sequence of cross sections of anlage of nasal apparatus of 29 mm long embryo, in rostrocaudal direction. 5,6 - sections of region of nostril and vestibule.

Slabý O.: Early morphogenesis of the nasal apparatus in the little grebe



7 — section of region of nostril and vestibule, 8, 9 — sections of region of main cavity of nasal tube.



10 - section of region of main cavity of nasal tube, 11, 12 - sections of region of choana and olfactory epithelium.

Abbreviations. A - aulax, C - cupula nasi ant. (contingently, cartilago parietotectalis), D - ductus nasolacrimalis, E - outer choana., H - main cavity of epithelial nasal tube, K - stem part of main cavity, M - maxilloturbinal, N - nostril, O - sacter (olfactory region), P - processus praenasalis, R - passage corresponding to descending arm of choanal passage in reptiles, S - septum nasi, V - vestibule, W - "Winkeltasche".

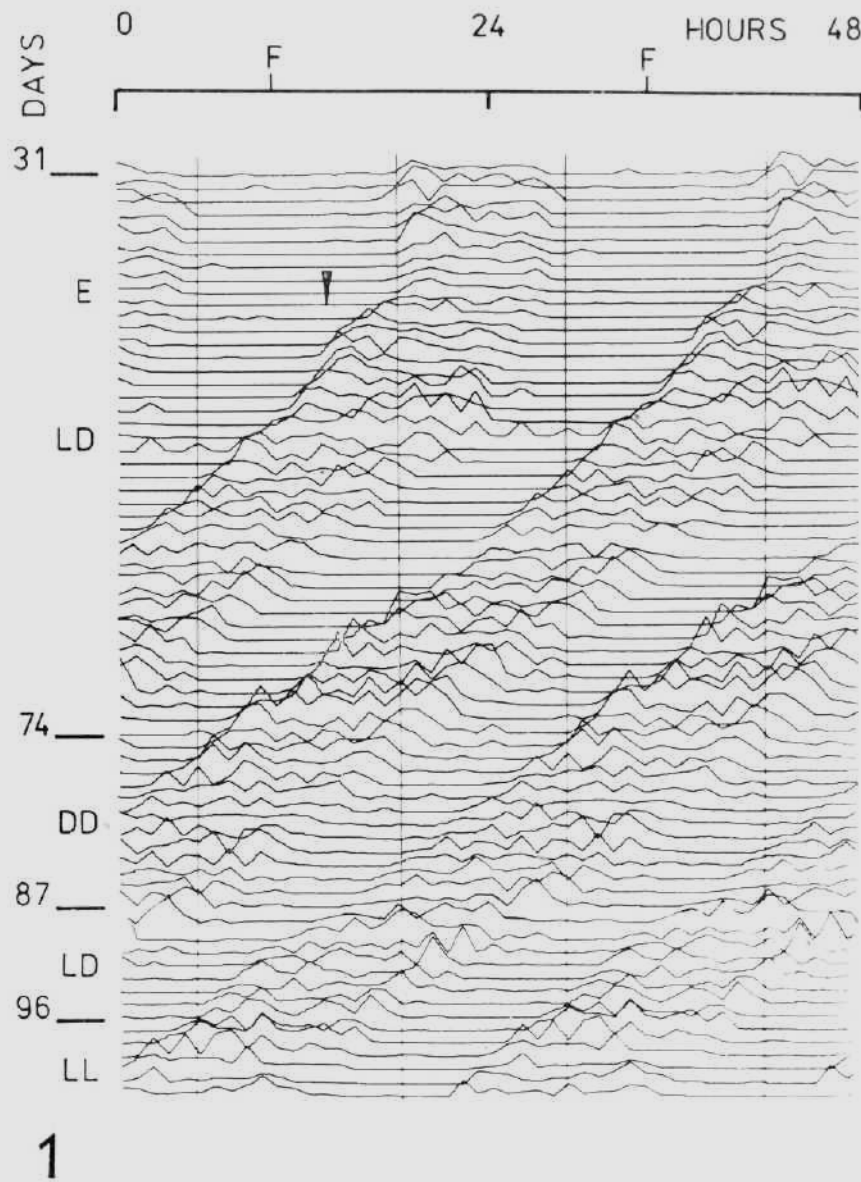


Fig. 1: An example of locomotor activity in *Crocidura suaveolens* (animal No. 7) before and after bilateral eye enucleation. E = day of eye enucleation; F = feeding at 10 o'clock.

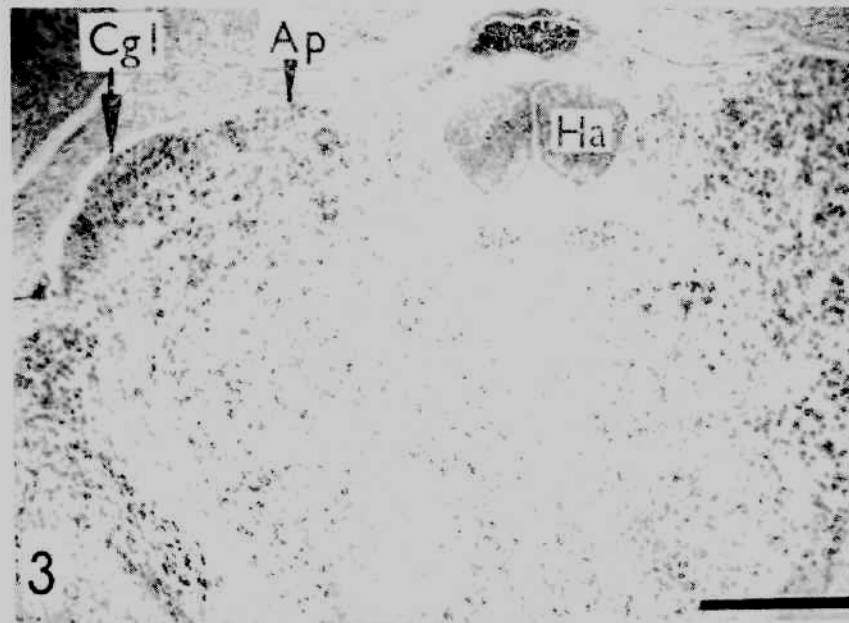
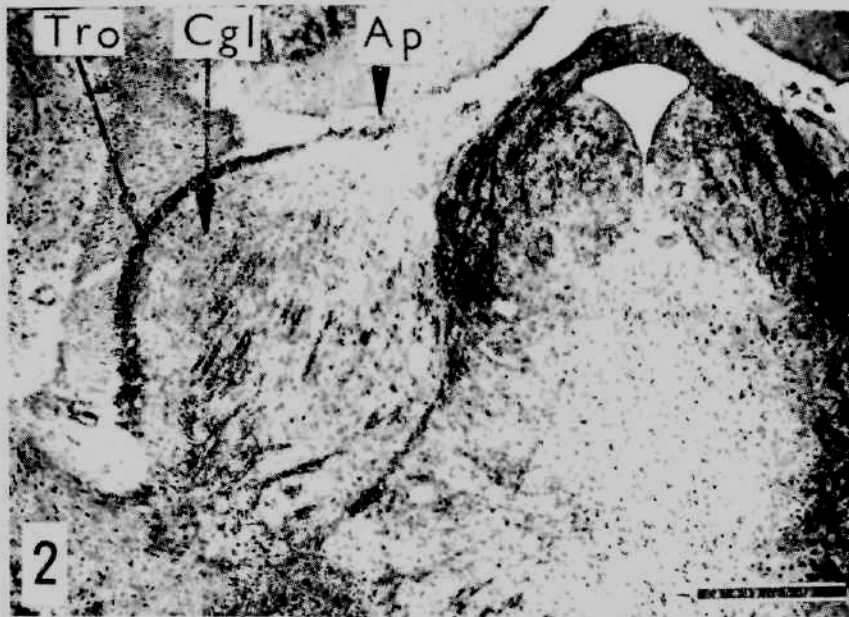


Fig. 2: Coronal section through the diencephalon at the level of commissura habenularum in animal No. 16/12. Tro = tractus opticus; Cgl = corpus geniculatum laterale; Ap = area pretektalis. Impregnated by Fink-Heimer's method. Bar = 400 μ m.

Fig. 3: Coronal section through the diencephalon of *Sorex araneus* (animal No. 36/83 1) at the level of nucleus habenulae (Ha) to show a Nissl-picture of the same situation as in Fig. 2. Further description in Fig. 2. Cresyl violet stain. Bar = 400 μ m.

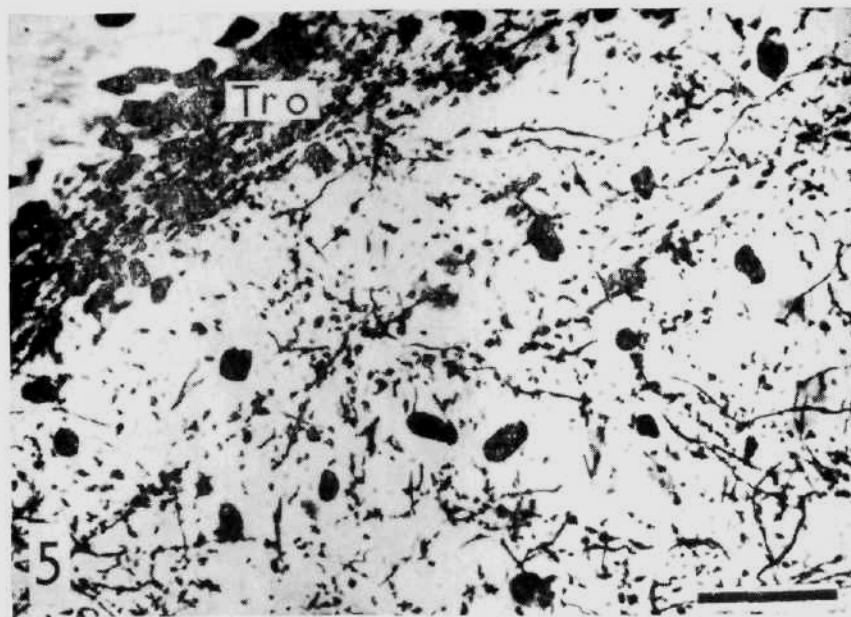
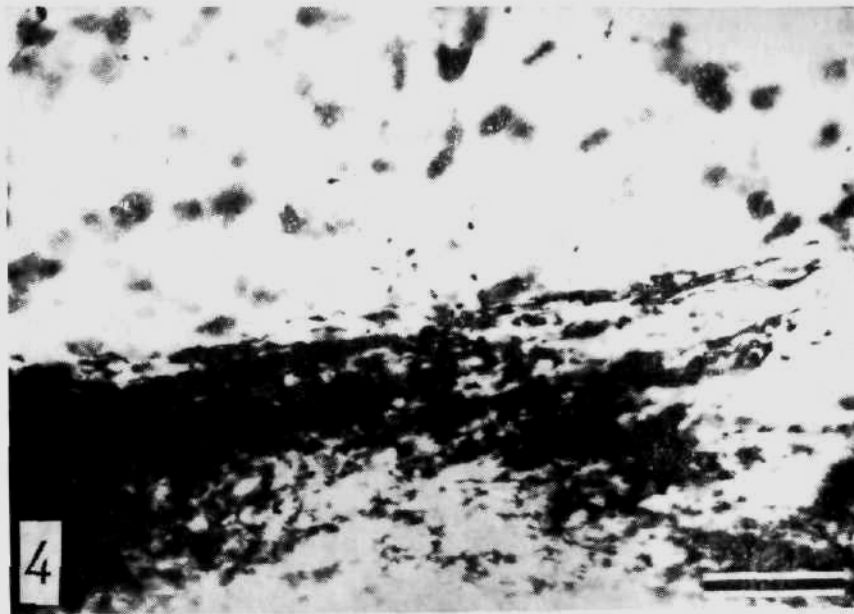


Fig. 4: Detail of chiasma opticum (right side) in animal No. 13/83 with degenerating fibers entering the dorsal part of hypothalamus. Impregnated by Fink-Heimer's method. Bar = 30 μ m.

Fig. 5: Detail of preterminal and terminal degenerations in the dorsal part of corpus geniculatum laterale (cf. arrow in Fig. 2). Impregnated by Fink-Heimer's method. Bar = 30 μ m.

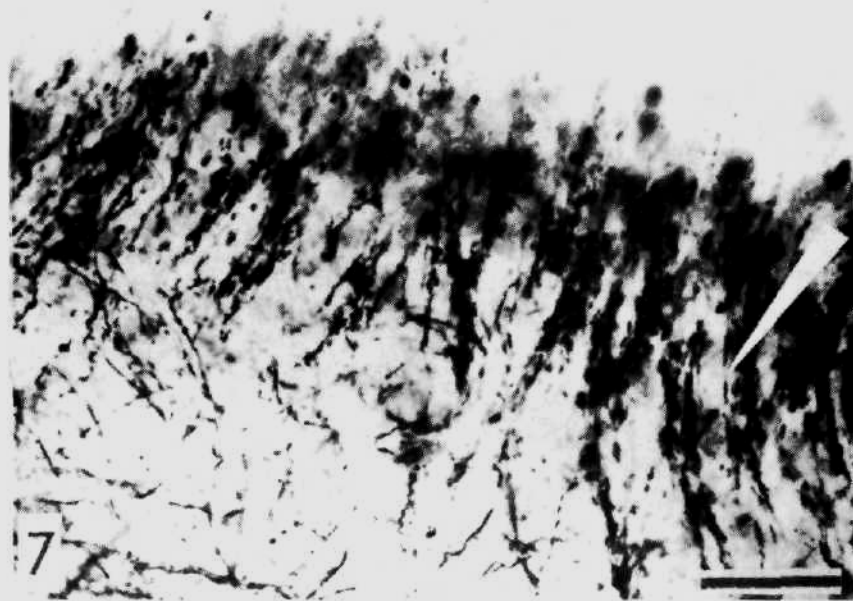


Fig. 6: Degenerating fibers entering the pretectal area (cf. arrow in Fig. 2). Impregnated by Fink-Heimer's method. Bar = 30 μ m.
Fig. 7: Preterminal degeneration seen in the stratum opticum and stratum griseum superficiale of the rostral colliculus in animal No. 1383. Arrow indicates coarse degenerated fibres of the optic tract. Impregnated by Fink-Heimer's method. Bar = 30 μ m.

POKYNY PRO AUTORY

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Hlavička práce. 1. Název pracoviště. 2. Název práce (u prací taxonomických v závorce za názvem systematické zařazení druhu nebo skupiny — např. Ostracoda: Cyprinidae), obojí v řeči, v níž je práce psána. 3. Jméno a příjmení autora.

Vlastní práce: 1. Velmi stručný abstrakt, v rozsahu nejvýše 15 řádek, v angličtině. 2. Úvod do problematiky (stručně). 3. Materiál a metodika (u známých metod pouze odkaz). 4. Vlastní část experimentální nebo popisná. 5. Diskuse. 6. Závěr. 7. Seznam citované literatury (nikoliv bibliografie!). 8. Adresa autora. 9. Tabulky, texty k obrázkům a grafům. Celý rukopis je průběžně stránkovan.

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V Praze 1984

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