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A New Species of *Gymnocephalus* (Pisces: Percidae) from the Danube, with Remarks on the Genus

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A new species of percoid fish, *Gymnocephalus baloni*, from the Czechoslovak stretch of the Danube River, is described together with hybrids between it and *Gymnocephalus cernua*. *Gymnocephalus baloni* appears to be exclusively a rheophilous species endemic to the Danube basin. The *G. cernua* population from the Danube seems to be mainly limnophilous while other populations from other basins over the whole range occupied by this species display both rheophilous and limnophilous patterns. Two subgenera of the genus *Gymnocephalus* are proposed and defined: Subgenus *Gymnocephalus* sensu stricto, comprising *G. schraetser* and *G. acerina* and subgenus *Acerina*, consisting of *G. cernua* and *G. baloni*. The former subgenus seems to be more primitive than the latter. Speciation within the subgenus *Gymnocephalus* has followed geographical isolation, while speciation in the subgenus *Acerina* probably resulted from ecological specialization. It is supposed that the Paleodanube (sensu Lindberg, 1955) was the center of origin and subsequent expansion of the genus *Gymnocephalus*.

THE genus *Gymnocephalus* Bloch (syn. *Acerina* Cuvier, *Cernua* Fleming, *Leptoperca* Gill, see Colette, 1963) has long been recognised as comprising three species. *Gymnocephalus cernua* (Linnaeus) inhabits northern and central Europe, including north-eastern France, England except Scotland and Ireland, the whole of eastern Eu-

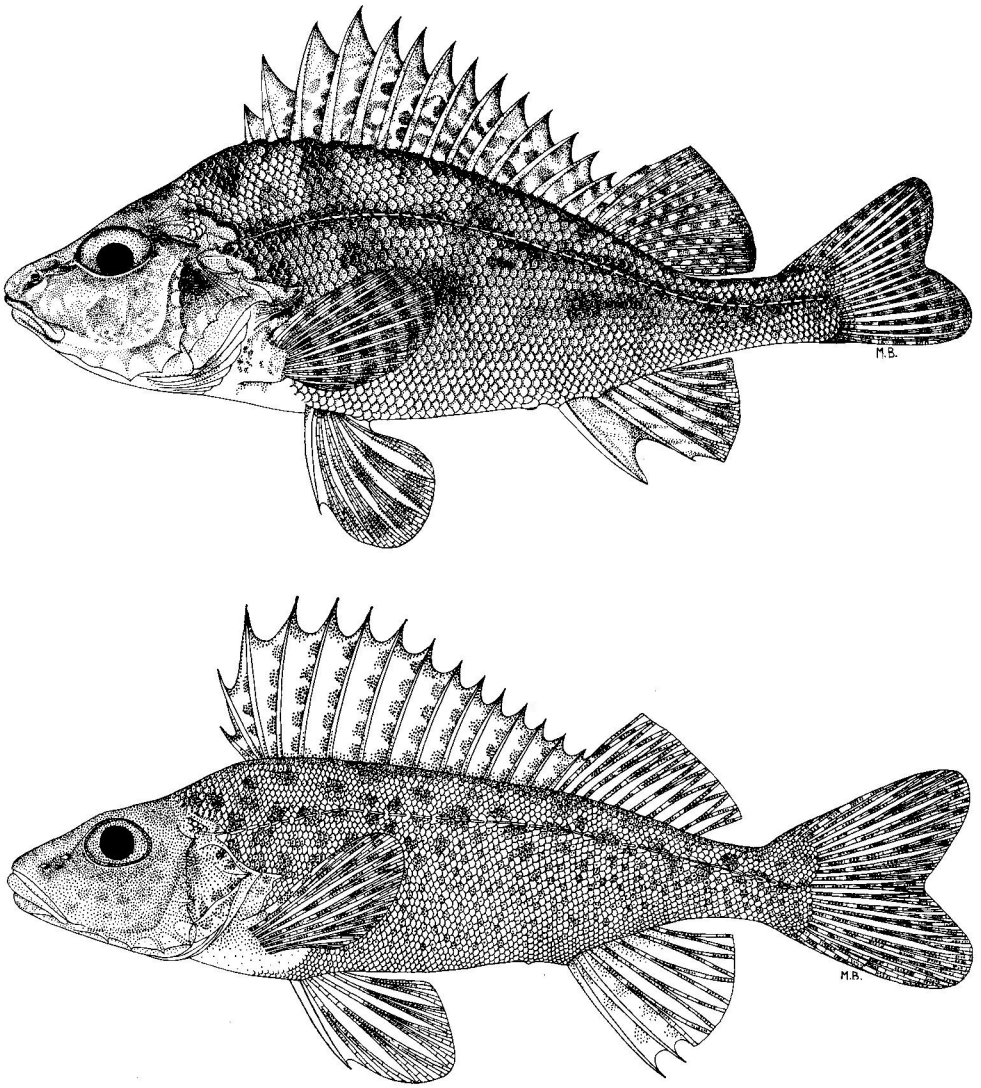

Fig. 1. Holotype of *Gymnocephalus baloni* n. sp. (above), a female of 103.7 mm SL, and a specimen of *G. cernua* (below), a female of 92.0 mm SL, *ex* Danube.

rope, the rivers entering the Baltic Sea, the rivers entering the White Sea, and all Siberia including the Kolyma River but excluding the Amur. *Gymnocephalus acerina* (Güldenstädt) is limited to the northern affluents of the Black Sea, i.e. Dniester, Southern Bug, Dnieper, Don, Donets and the delta of the Kuban River. *Gymnocephalus schraetser* (Linnaeus) is endemic to the Danube and Kamchia rivers, the latter in Bulgaria. In the summer of 1970 a new, fourth species was discovered in the Czechoslovak stretch of the Danube River. Its description, and observations on other species, resulting in the recognition of two groups within the genus *Gymnocephalus*, are the subjects of the present paper.

Gymnocephalus ***baloni*** sp. n.
Hrebenačka Balonova (Slovak name)
Balon's ruffe (Proposed English name)
Figs. 1, 3, 4

There are a few previous references that seem to apply to this species. Thus Antipa

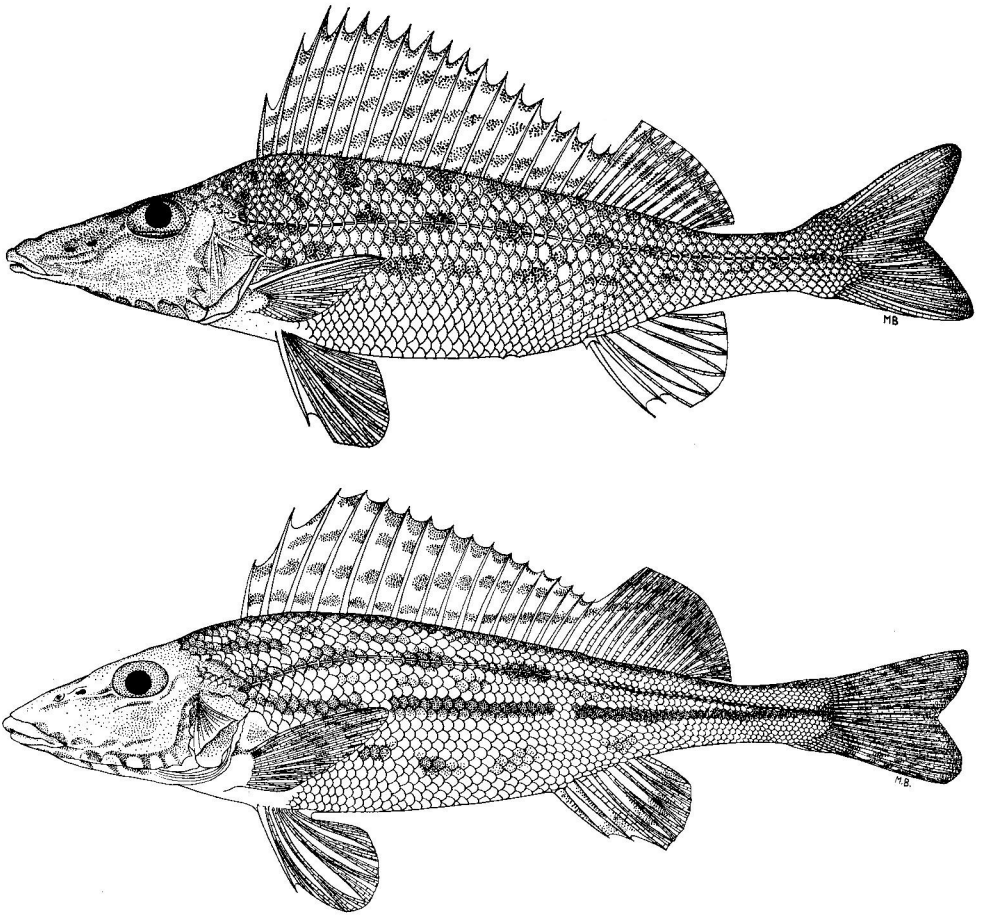

Fig. 2. *Gymnocephalus acerina* (above), a female of 132 mm SL *ex* Dneiper River, and *G. schraetser* (below), a female of 168 mm SL *ex* Laborec River.

(1909) introduced a figure (his fig.) of a ruffe from the Danube River in Roumania which evidently belongs to *G. baloni*. This figure was used also by Berg (1949) and Bănărescu (1964). Day's drawing of *G. cernua* (1880, pl. 3) looks like *G. baloni*, but the description relates to *G. cernua*. (He visited European museums and may have taken his drawing from a specimen in one of them—Dr. E. Trewavas, in litt. 7 June 1972.) Also Heckel and Kner (1858) introduced a figure of *G. cernua* (their fig. 6), which in some respects looks like *G. baloni*; the description, however, belongs to the first species. A drawing of *G. cernua* published by Schindler (1953), which has been used also by the British Museum (Natural History), London, for colored post-cards (M 28), is similar to the hybrid between *G. baloni* and *G. cernua*. Vladykov (1931) described *Acerina cernua* natio *danubica* from samples evidently composed of *G. cernua* and *G. baloni*.

Holotype.—Female, 107.3 mm SL, ichthyological collection of the Slovak National Museum at Bratislava (SNM-RY), no. 2261. Caught in the Danube River near Kližská Nemá, Slovakia, 25 Oct. 1968 by K. Hensel.

Paratypes.—SNM-RY 2262, 10 specimens (5 males, 5 females) and CU-RY 196, 20 specimens (9 males, 11 females), all caught with the holotype. Size of paratypes 56.6–121.2 mm SL; 17 specimens measured.

Other material.—None of the following is designated as type material: ZICU 8, (1) (originally determined as *Acerina cernua* natio *danubica*), Vojany, East Slovakia, 8

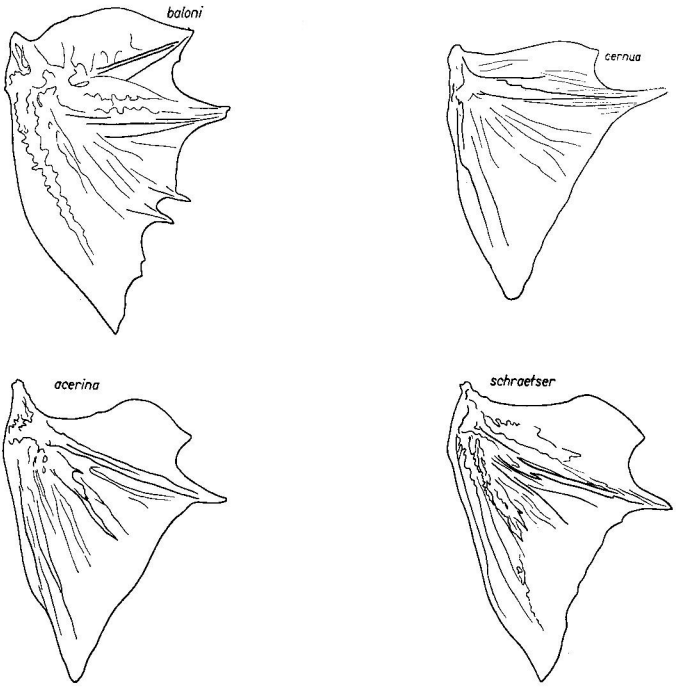

Fig. 3. Opercula of species of *Gymnocephalus*. A. (upper left) *G. baloni*; B. (upper right) *G. cernua*; C. (lower left) *G. acerina*; D. (lower right) *G. schraetser*. Note additional spines in *G. baloni*.

Dec. 1928; LFRH 98283, (5) Danube (backwater Vojka-Žofín), Slovakia, 7–17 Sept. 1970; CU-RY 356, (2), Danube at Čilizská Radvaň, Slovakia 14 Aug. 1970; CU-RY 212, (1), Danube at Kližská Nemá, Slovakia, 20 Nov. 1968; CU-RY 81, (1), Danube near Radvaň nad Dunajom, Slovakia, March–May 1968.

Specimens seen but not measured, all originally determined as *A. cernua*: IBTS 2227, (2) Danube at Bertrasca, Roumania, 14 Aug. 1965; LFRH 98287, (45), Timis River at Peciul Nou, Roumania, 16 Sept. 1965; LFRH 98284, (21), Timis River at Peciul Nou, Roumania, 28 Sept. 1970; LFRH 98285, (4), delta of Danube River at Ivancea, Roumania, 17 April 1965.

Diagnosis.—Distinguished from all other species of the genus by having 4–6 dark transverse bands on the flanks, sometimes vaguely delimited. Body robust, short and deep, nape covered by scales, opercle with 2 spiny processes.

Description.—D. XIV–XV (XVI), (10) 11–12; A. II (4) 5–6; pored scales in lateral line (35) 36–37 (38) (39); gillrakers (9) 11–13 (14), short; preopercular spines (9) 10–13 (14). Opercle with two distinct spines (Fig. 3). Subopercle short, beak-like, with serrated lower edge (Fig. 4). Branchiostegals 6–7 (8). Vertebrae 33–35.

Body robust, short and deep, 31.0% (28.9–35.2) of standard length. Head short, blunt, steeply continuing into body. In bigger specimens there is a characteristic hump. Pelvics, pectorals and anal fin, as well as lower lobe of caudal fin, usually eroded and regenerated. Front edge of base of pelvics situated behind hind edge of base of pectoral fins. Upper edge of soft part of dorsal fin nearly perpendicular to line of caudal peduncle. Spinous rays of anal fin stout, slightly but distinctly bent; first spine usually shorter than second. Upper edge of eye mostly above head profile.

Measurements of the holotype, 17 paratypes and other material are shown in Table 1.

Coloration in formalin.—Head and body yellowish-brown, darker on flanks and yellow

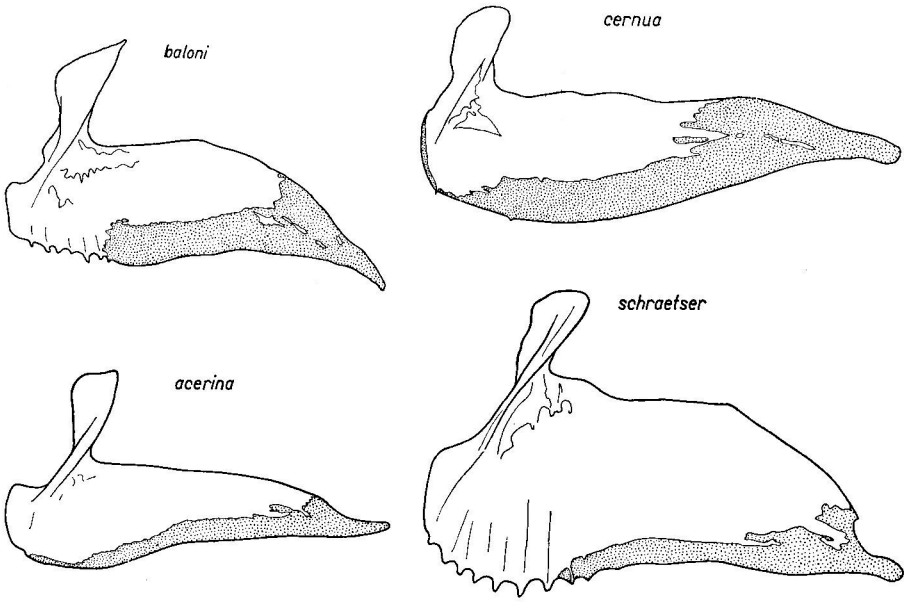

Fig. 4. Subopercula of species of *Gymnocephalus*. A. (upper left) *G. baloni*; B. (upper right) *G. cernua*; C. (lower left) *G. acerina*; D. (lower right) *G. schraetser*.

on belly. Scales bordered by small dark greyish-brown spots. A darker irregular band of variable width present along lateral midline of body, but often indistinct, the band usually formed by irregular spots bigger than the diameter of the eye. Along the back are 4–6 spots which continue downwards and gradually lose their intensity. The bands thus formed are similar to those in *Perca fluviatilis*. Belly usually yellowish but always pigmented with small brown spots. Head above line of lower edge of the eye greyish-brown, cheeks and opercles pigmented with small dark spots. Dorsal, caudal and anal fins compactly spotted. A large unbordered dark blotch on base of anterior edge of dorsal fin. A vague V-shaped dark spot on top of head.

Ecology.—There are as yet no detailed data on the ecology of *G. baloni* sp. n., but some preliminary observations point to an exclusively rheophilous habit. In 1969 in the backwater called Žofín-Vojka, some 40 km below Bratislava, which is part of the larger arm Vojka and 1.5 km from the outlet of the latter into the Danube River, this species had not been recorded. In the spring of 1970 a breach occurred in the left-bank of this arm so that it became directly connected with the main stream of the Danube. The current velocity of the arm reached 0.66 m/sec. The original fish fauna changed and showed both an absolute and relative increase in the number and density of rheophilous species, among which appeared *G. baloni* and *G. schraetser*. In the autumn of the same year, the water level sank so that communication with the main stream of the river was interrupted again. An estimate of the population density, by the mark-and-recapture method, was 125 specimens of *G. cernua* per hectare, weighing 0.26 kg/ha. In the spring of 1971, the breach was repaired and the mouth of the main arm filled up so that the whole Vojka arm-complex changed into one of closed water. Moreover, the water level that year was much lower than in the previous year. Despite intensive search, we were again unable to find *G. baloni*. Beside other species, the arm was occupied by the limnophilous *G. cernua* and by remnants of the rheophilous *G. schraetser* population. The density of the latter in the summer of 1970 was 140 specimens/ha, weighing 2.86 kg/ha; in autumn of the same year, 156 specimens/ha, weighing 1.35 kg/ha, but only 5 specimens/ha, weighing 0.03 kg/ha in July

TABLE 1. COUNTS AND MEASUREMENTS OF *Gymnocephalus baloni* SP.N.

	Holotype	Paratypes		ZICU 8[1]	Type material + other specimens measured /n=28/	
		x̄	Ranges		x̄	Ranges
Standard length (mm)	107.3	96.5	56.6–121.2	112.6	93.7	56.6–121.2
Spines in D	15	14.9	14–16	15	14.9	14–16
Soft rays in D	11	11.4	10–12	11	11.2	10–12
Spines in A	2	2.0	2–2	2	2.0	2–2
Soft rays in A	5	5.6	5–6	6	5.5	4–6
Scales in lateral line	36	36.6	35–39	36	36.4	35–39
Gill-rakers	14	12.1	11–13	13	12.2	11–14
Preopercular spines	13	11.1	9–14	13	11.4	9–14
Opercular spines	2	2.0	2–2	2	2.0	2–2
Branchiostegals	7	6.9	6–8	6	6.9	6–8
Vertebrae[2]					34.1	33–35
In % of standard length						
Head length	23.6	30.1	27.7–31.8	35.1	30.5	27.7–35.1
Snout length	10.2	10.1	9.1–11.5	11.3	10.1	8.8–11.7
Diameter of eye	8.6	8.6	7.6–9.5	10.1	8.9	7.6–10.1
Postorbital distance	12.8	12.6	11.6–13.3	14.1	12.6	11.6–14.7
Head depth	26.9	25.8	24.7–27.6	28.8	25.9	24.3–28.8
Head width	29.8	27.3	25.6–30.0	26.8	28.0	25.6–33.9
Interorbital distance	7.5	7.4	6.6–8.9	8.2	7.3	6.4–9.1
Predorsal distance	35.3	33.8	32.1–35.6	40.0	34.4	32.1–40.0
Preventral distance	39.4	39.1	36.6–40.3	41.7	38.8	35.7–41.8
Preanal distance	70.3	70.3	66.8–72.1	77.8	70.2	66.1–77.8
Body depth	31.6	31.2	28.9–32.7	35.2	31.0	28.9–35.2
Caudal peduncle length	18.6	19.7	16.2–23.0	22.4	19.9	16.2–23.0
Minimal body depth	8.4	8.7	8.2–9.6	10.4	8.7	7.9–10.4
Distance P-V	12.6	12.3	11.0–13.0	12.9	12.1	9.7–13.5
Distance V-A	32.7	34.7	33.0–38.0	38.6	34.3	31.4–38.6
Length of D	58.2	56.4	52.5–60.1	64.8	56.7	52.5–64.8
Length of A	13.9	14.4	12.8–16.2	18.0	14.5	12.8–18.0
Length of C_1	19.9	20.2	16.8–22.5	24.5	20.6	16.8–24.5
Length of C_2	18.1	19.6	17.5–21.6	22.1	19.6	17.0–22.1
Length of P	20.1	19.4	17.6–22.3	23.8	19.8	17.5–23.8
Length of V	22.3	21.4	18.2–23.8	24.8	21.9	18.2–24.8
Depth of spinous D	18.2	18.2	16.5–21.6	23.4	18.9	16.5–23.4
Depth of soft D	15.5	15.7	14.3–17.3	18.0	16.1	14.3–20.5
Depth of A (first spine)	14.5	14.4	11.9–18.6	17.1	14.9	11.9–20.7
Base of A to anus	5.0	4.3	3.2–5.6	6.3	4.6	3.2–6.3

[1] Vladykov's *Acerina cernua* n. *danubica*
[2] 13 specimens X-rayed, 2 stained

1971, and no specimens of this species were found in October 1971. The holotype and paratypes of *G. baloni* were caught among the dam stones in the main stream of the Danube River at Klížská Nemá. However, here it was found only in places where the stones were directly washed by the current. The eroded fins in most of the material examined also point to the rheophilous habits of this species. It should be men-

TABLE 2. MAIN COUNTS AND MEASUREMENTS OF *Gymnocephalus cernua* × *Gymnocephalus baloni* HYBRID AND ITS RELATION TO THE PARENTAL SPECIES EXPRESSED BY A HYBRID INDEX (*G. cernua* = 0, *G. baloni* = 100). Based on 26 specimens of *G. baloni*, 25 of *G. cernua*, and 11 hybrids.

Species	*G. cernua*	*G. cernua* × *G. baloni*	*G. baloni*	Hybrid Index
Spines in D	13.9 (12–15)	14.6 (14–15)	14.9 (14–16)	70
Soft rays in D	12.3 (10–14)	11.5 (10–13)	11.2 (10–12)	73
Soft rays in A	4.8 (4–6)	5.0 (4–6)	5.5 (4–6)	29
Lateral line	35.0 (34–37)	35.6 (34–38)	36.4 (35–39)	43
Gill-rakers	10.4 (8–12)	11.7 (10–14)	12.1 (11–13)	77
Preopercular spines	9.2 (8–11)	10.2 (8–13)	11.3 (9–14)	48
Diameter of eye	8.1 (6.6–8.8)	8.3 (7.4–9.9)	8.9 (7.6–9.8)	25
Interorbital distance	6.1 (5.3–7.7)	7.2 (6.3–8.1)	7.3 (6.4–9.1)	92
Head depth	22.4 (20.9–24.1)	23.8 (19.4–26.3)	25.7 (24.3–27.6)	42
Head width	25.0 (21.2–29.6)	24.8 (22.1–27.9)	28.0 (25.6–33.9)	7
Predorsal distance	32.7 (30.7–34.8)	34.8 (32.2–39.1)	34.1 (32.1–37.0)	150
Preventral distance	36.4 (33.0–38.6)	36.6 (34.5–39.3)	38.7 (35.7–41.8)	9
Body depth	25.8 (24.1–27.3)	30.2 (26.7–35.1)	30.8 (28.9–32.7)	88
Caudal peduncle length	21.6 (20.1–24.5)	20.9 (26.7–35.1)	19.8 (28.9–32.7)	39
Minimal body depth	8.2 (7.7–8.9)	8.9 (8.2–9.5)	8.6 (7.6–9.6)	175
P-V distance	9.7 (7.7–11.2)	11.5 (9.8–13.3)	12.0 (9.7–13.5)	78
Length of D	53.8 (49.9–55.6)	57.0 (54.8–58.9)	56.3 (52.5–58.9)	128
Length of A	12.5 (10.5–14.4)	13.4 (10.6–15.8)	14.4 (12.8–16.2)	47
Depth of soft D	14.3 (12.4–17.4)	15.0 (12.6–17.7)	16.1 (14.3–20.5)	39

Mean hybrid index for counts	49
Mean hybrid index for measurements	70
General average of hybrid indices	60

tioned, however, that specimens from the Danube delta, the River Timis at Peciul Nou and from the Latorica River at Vojany did not display this erosion.

Distribution.—According to our preliminary investigations *G. baloni* seems to be limited to the Danube Basin. We have found it among fishes from the Danube in Czechoslo-

TABLE 3. DIFFERENCES BETWEEN *Gymnocephalus baloni* AND *Gymnocephalus cernua* AND BETWEEN *Gymnocephalus cernua* SAMPLES FROM THE DANUBE RIVER AND SWEDEN RESPECTIVELY, EXPRESSED IN t TEST AND COEFFICIENT OF DIFFERENCE (UNDERLINED FIGURES STATISTICALLY SIGNIFICANT).

	G. baloni vs.								*G. cernua* (Danube) vs.			
	G. cernua (Sweden)				*G. cernua* (Danube)				*G. cernua* (Sweden)			
	n_1+n_2-2	t	P	C.D.	n_1+n_2-2	t	P	C.D.	n_1+n_2-2	t	P	C.D.
Spines in D	37	2.07	0.50	–	49	6.39	0.001	0.90	36	2.82	0.010	0.47
Soft rays in D	37	3.85	0.001	0.62	49	5.65	0.001	0.80	36	0.72	0.500	–
Soft rays in A	37	0.92	0.400	–	49	7.20	0.001	1.57	36	2.46	0.025	–
Preopercular serrae	37	1.72	0.100	–	49	6.47	0.001	0.84	36	2.64	0.025	–
Branchiostegals	37	3.93	0.001	0.65	49	0.82	0.500	–	36	1.20	0.400	–
Gill-rakers	37	7.88	0.001	1.37	47	6.24	0.001	0.68	36	0.29	–	–
Lateral line	37	0.27	–	–	49	4.83	0.001	0.93	35	4.17	0.001	0.71
Head length	37	1.90	0.100	–	49	0.59	–	–	36	3.39	0.005	0.56
Snout length	37	0.82	0.500	–	49	1.02	0.400	–	36	0.00	–	0.00
Diameter of eye	37	2.85	0.010	0.46	49	5.06	0.001	0.70	36	6.42	0.001	1.04
Interorbital distance	37	7.25	0.001	1.33	49	8.28	0.001	0.92	36	3.92	0.001	0.37
Postorbital distance	37	0.47	–	0.08	49	2.09	0.050	–	36	0.94	0.400	–
Head depth	37	3.34	0.005	0.55	49	13.22	0.001	1.87	36	0.33	–	–
Predorsal distance	37	2.56	0.025	–	49	4.42	0.001	0.63	36	6.23	0.001	1.02
Preventral distance	37	7.86	0.001	1.35	49	5.76	0.001	0.82	36	4.45	0.001	1.73
Preanal distance	37	2.07	0.050	–	49	2.51	0.025	–	36	0.28	–	–
Body depth	37	4.90	0.001	0.80	49	18.68	0.001	2.68	36	1.26	0.400	–
Caudal peduncle length	37	3.74	0.001	0.62	49	4.71	0.001	0.67	36	0.61	–	–
Minimal body depth	37	0.95	0.400	–	49	4.14	0.001	0.59	36	3.013	0.005	0.50
P-V distance	37	4.54	0.001	0.72	49	9.19	0.001	1.29	36	0.95	0.400	–
V-A distance	37	3.70	0.001	0.06	49	0.66	–	–	36	0.77	0.500	–
Length of D	37	3.10	0.005	0.49	49	3.25	0.001	0.78	36	0.72	0.500	–
Length of A	37	0.35	–	0.06	49	6.76	0.001	0.95	36	1.96	0.100	–
Length of P	37	5.52	0.001	0.95	49	1.52	0.200	–	36	6.82	0.001	1.17
Length of V	32	2.77	0.010	0.51	49	0.22	–	–	36	8.64	0.001	0.25
Depth of spinous D	37	0.13	–	0.02	49	2.21	0.050	–	36	1.08	0.400	–
Depth of soft D	37	3.04	0.005	0.49	49	4.80	0.001	0.68	36	0.19	–	–
Depth of A	36	2.09	0.500	–	49	2.53	0.025	–	32	0.40	–	–
Base of A–anus	37	2.01	0.100	–	49	2.58	0.025	–	36	0.31	–	–

vakia as well as from the Danube delta in Roumania some 1800 km downstream. It was absent, however, in a sample from the Danube in Bavaria (Straubing). *G. baloni* obviously also inhabits the bigger rivers and lower courses of rivers in the Danube Basin, as one can conclude from its presence in the Latorica River at Vojany, Slovakia and in the Timis River at Peciul Nou in Roumania. Samples originating from Sweden, England, Germany and North Asia (Ob River in the USSR) were composed exclusively of *G. cernua*. Thus it is presumed that *G. baloni* is among the Danubian endemics,[1] being distributed in the middle and lower Danube and the middle and lower courses of some of its tributaries (Fig. 11). The exact range of this species, however, needs more detailed investigation.

Etymology.—This new species is named after Dr. Eugeniusz K. Balon, our friend and former collaborator, who initiated extensive ichthyological investigations of the Czechoslovak section of the Danube River 15 years ago.

Hybrids.—G. baloni seems to hybridize with *G. cernua*. A sample taken in the mouth of an arm of the Danube River in July 1965 at Karlova Ves (western side of Bratislava) consisted of 11 specimens (6 females and 5 males) measuring 73.2–137.5 mm SL. These fish are intermediate in most of the characters in which the two species differ (Table 2). Calculated hybrid indices (Hubbs and Kuronuma, 1942) show a great variation, while most of the features, as well as the mean values, are only slightly shifted towards one of the parental species, they show the intermediate position of the hybrids in these parameters. Investigated osteological characters also clearly show that this sample is of hybrid origin, as does coloration, which is intermediate between the presumed parental species.

Comparison with other populations and species.—For comparison, samples derived mostly from populations of *G. cernua* were used. In some cases, Student's "t" test was applied. The results are summarized in Table 3. It can be seen that there are differences in counts and measurements between *G. baloni* and populations of *G. cernua*. For practical purposes, however, the only useful measurement is that of body depth and the only count that of gill rakers. Among other characters, the shape of the dorsal margin of the dorsal fin, perpendicular to the caudal peduncle in *G. baloni* but oblique in *G. cernua*, is a "key feature." It is of interest, however, that there are bigger differences between samples of *G. baloni* and *G. cernua* from the Danube basin than between the former and samples of *G. cernua* from other drainages. In fact, the counts and measurements of *G. baloni* are similar to or identical

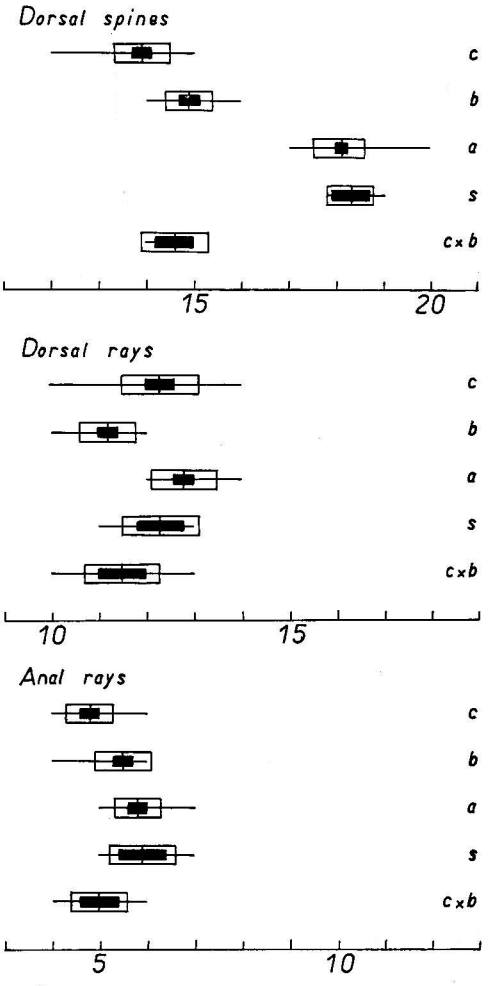

Fig. 5. Comparison of number of dorsal spines and dorsal and anal rays respectively in *Gymnocephalus cernua* (c), *G. baloni*, (b), *G. acerina* (a), *G. schraetser* (s) and in the hybrid of *G. cernua* and *G. baloni* (c × b). *G. cernua* shown in this figure as well as in all other ones from the Danube.

[1] A recent paper in Voprosy ikhtiologii suggests that *G. baloni* may live in the Dnieper (USSR).

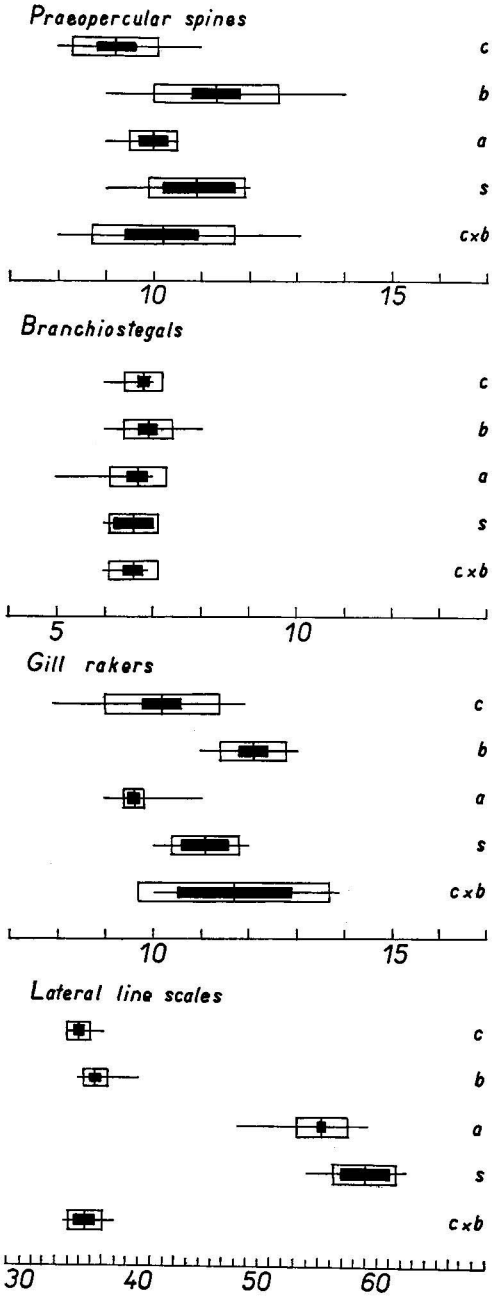

Fig. 6. Comparison of the number of preopercular spines, branchiostegals, gill rakers and lateral line scales in species of the genus *Gymnocephalus*. (Abbreviations as in Fig. 5.)

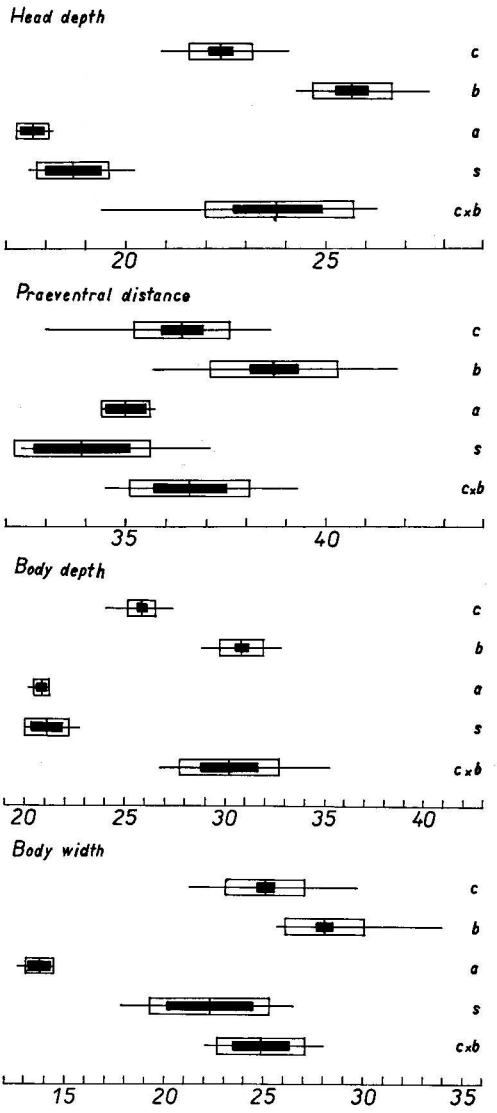

Fig. 7. Comparison of head depth, preventral distance, body depth and body width in per cents SL in species of the genus *Gymnocephalus*. (Abbreviations as in Fig. 5.)

with those of samples of *G. cernua* from basins other than the Danube. The most striking differences are in coloration and in some osteological features (Fig. 1–4), as well as in ecology. From the known data on the biology of *G. cernua*, we can conclude that populations of this species in the Danube River are mostly limnophilous, but those in other river basins are both limno- and rheophilous.

Figs. 5–9 show that *G. baloni*, in its morphological features, stands between *G. cernua* and *G. acerina* in number of spines in the dorsal fin, number of rays in the anal fin and in the number of scales in the lateral

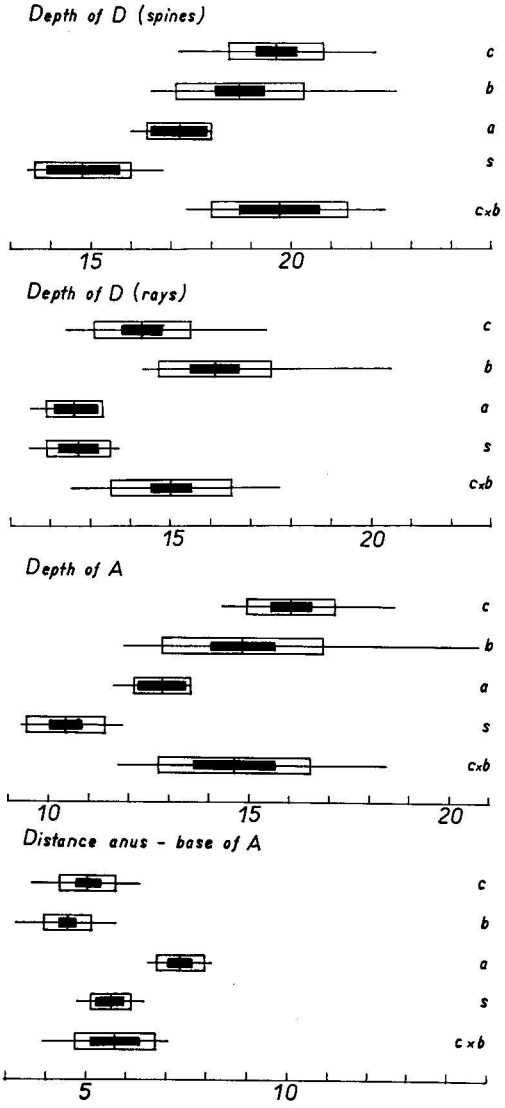

Fig. 8. Comparison of caudal peduncle length, P-V distance, length of D and length of A in % of standard length in species of the genus *Gymnocephalus*. (Abbreviations as in Fig. 5.)

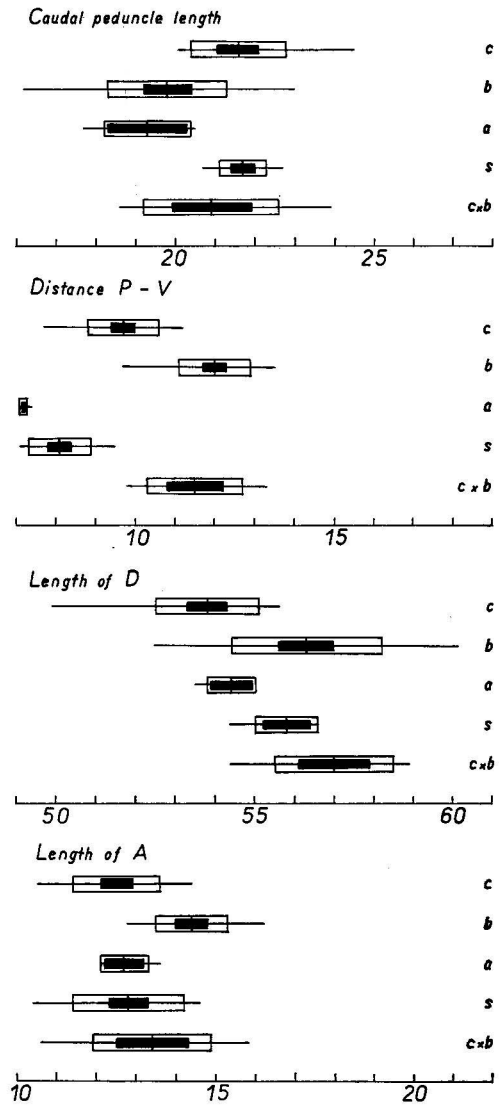

Fig. 9. Comparison of dorsal and anal fin depth and distance from anus to the base of A in % SL in species of the genus *Gymnocephalus*. (Abbreviations as in Fig. 5.)

line (here, of course, it stands closer to *G. cernua* than to *G. acerina*). In the number of branched rays in the dorsal fin, *G. baloni* is closer to *G. schraetser*, as well as in the number of preopercular spines, the number of branchiostegals and in the number of gill rakers. Opercle shape is quite different (Fig. 3), and in this feature *G. baloni* stands apart from the other three species of the genus. The form of the suboperculum bears some resemblance to that of *G. schraetser* (Fig. 4), mainly in the general shape of this bone and in the presence of serrations on its lower edge.

Discussion.—The systematic status of some populations of *G. cernua* seems to be well known. Vladykov (1931) described natio *danubica* from the Tisa River (Danube basin) and Burmakin (1941) proposed ssp. *essipovi* for populations inhabiting Gydan Bay and the neighbouring rivers (Gydan

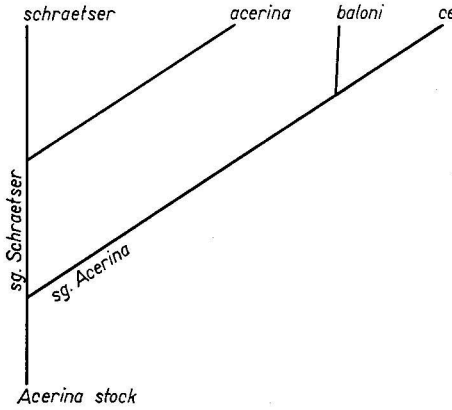

Fig. 10. Presumed phylogeny of the genus *Gymnocephalus*.

peninsula between the mouths of the Ob and Yenisei rivers). Berg (1949), however, synonymized both with the nominate form. Later Oliva (1953), Šimek (1959), Šafránek (1962) and Brtek and Rothschein (1964) repeatedly pointed out the differences between the Danubian populations and those inhabiting other river basins. These differences were seen in the number of scales in the lateral line, coloration, and body depth. According to Vladykov (1931), Oliva (1953) and Šafránek (1962) Danubian fish exhibit a shift to a smaller number of scales in the lateral line. Body depths in the Danubian population are bigger, according to Oliva (1953) and Šimek (1959), but smaller according to Brtek and Rothschein (1964). The latter authors also emphasized the different coloration of the Danubian fish, which is very similar to that of *G. acerina*, i.e., a number of distinct spots arranged in regular rows. It is evident that these authors were using the name *G. cernua* for both species: Oliva (1953), Šafránek (1962) and Brtek and Rothschein (1964) had *G. cernua* because they noted a low number of scales and recorded spots on the flanks. Šimek (1959) had *G. baloni* because of the deep body in his specimens. Also, Antipa (1909) must have had *G. baloni* in his hands, as his drawing of a fish from the Danube delta in Roumania is clearly *G. baloni* and not *G. cernua*. Vladykov (1931), when he described *G. cernua* n. *danubica*, had samples composed of both species, as is evident from his description (1931:343): "Tete, corps, nageoires impaires couverts de petites taches sombres, tres denses; parfois ces taches sont groupes en 6–7 bandes transversales peu marques." And (later:343): "Hauteur maxime du corps contenue de (3.0) 3.2 a 3.6 (3.8) fois dans sa longeur. . ." (i.e. 26.3–33.3%, mostly 27.8–31.3% of SL). Unfortunately, from 11 specimens examined by Vladykov, we were able to find only one (listed below under coll. no. ZICU 8), which is a female of *G. baloni* measuring 112.6 mm. *G. baloni* cannot be a hybrid between *G. cernua* and *Perca fluviatilis* (although the transverse bands of *G. baloni* are very similar to those of *P. fluviatilis*), since Kammerer (1907) and Nikolyukin (1952) showed that hybridization of these two species is impossible in nature. The artificially obtained reciprocal offspring died mostly during embryonic development and only rarely reached the larval stage.

Because *G. cernua* from the Danube basin seems to stand apart from populations in other watersheds, we have investigated the degree of difference with the possibility of ranking natio *danubica* as a subspecies. Comparison was made with a sample from Sweden, which is supposed to be the nominate form from the *terra typica*. (It is true that Linnaeus, 1758, wrote "in Europae lacubus" when mentioning the habitat of *G. cernua*, but for comparative purposes the sample of ruffe from Sweden was chosen to provide the pure limnophilo-rheophilous strain with no incidental influence from *G. baloni*). We used both the "t" test and the coefficient of difference. The results obtained (Table 3) show some significant differences between these two populations, but almost entirely on the basis of the t-test. Therefore the Danube population is not considered to be a subspecies. There is also great variability in several features, but with a broad overlap with populations from other river basins. Moreover, we have found statistical differences between nearly all populations, but these differences do not show any regular geographic correlation. Throughout, one can find certain differences from the nominate form. This, in our opinion, could well indicate the first phase in speciation. Of great interest is the difference in ecology. The population of the Czechslovak portion of the Danube basin is predominantly limnophilous, whereas other forms are both rheo- and limnophilous.

When counts and measurements of all 4 species of the genus *Gymnocephalus* are plotted (Figs. 5–9), one can see an apparent

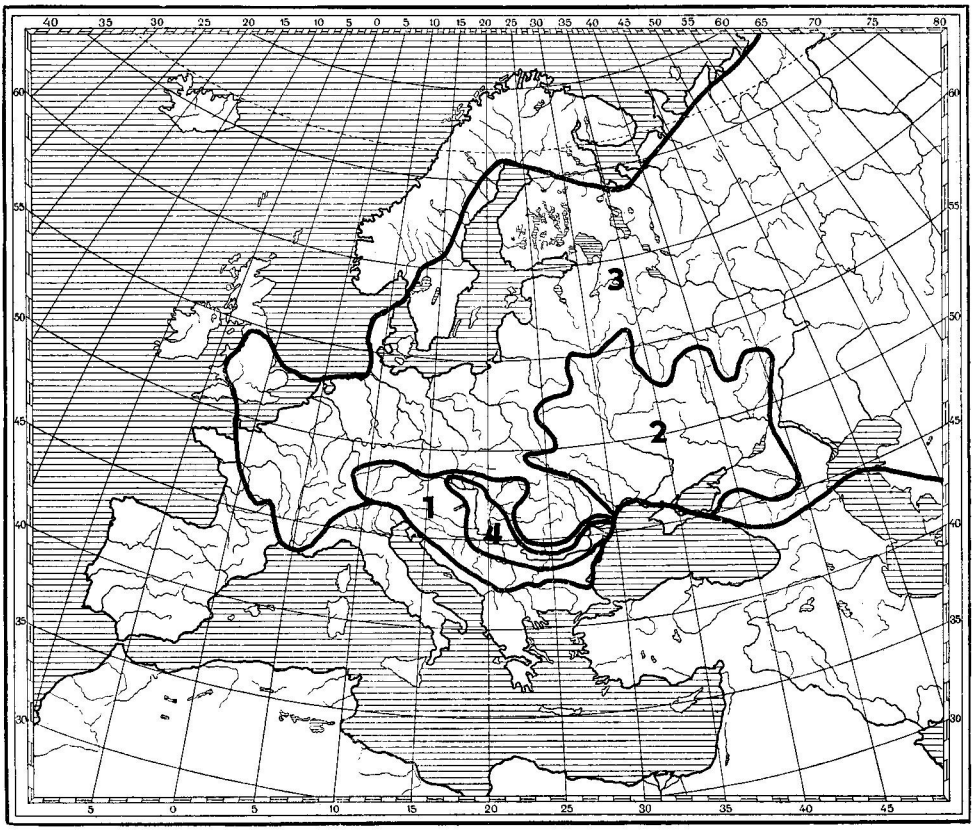

Fig. 11. Area of distribution of the genus *Gymnocephalus*. 1—*G. schraetser*, 2—*G. acerina*, 3—*G. cernua* (only part of its Asiatic distribution), 4—*G. baloni*.

separation into two groups. One group is composed of *G. cernua* and *G. baloni* and the other consists of *G. schraetser* and *G. acerina*. A similar grouping is obtained in respect to the number of vertebrae. Our observations combined with the data of Collette (1963) and Zhukov (1965), show that *G. cernua* has 32–38, *G. baloni* 33–35, but *G. schraetser* 38–40 and *G. acerina* 37–42 vertebrae. The two groups are also separated by color pattern: spots and transverse bands against longitudinal stripes and longitudinal rows of regular spots (Figs. 1 and 2). A close relationship between *G. acerina* and *G. schraetser* has also been noted by Jakubowski (1967), who studied the lateral line system of ruffes and found that in the structure of the neuromasts these species are mutually more similar that is either to *G. cernua*. Considering these facts we divide the genus *Gymnocephalus* into two *subgenera*:

Genus *Gymnocephalus* Bloch

1) Subgenus *Gymnocephalus* sensu stricto (syn. *Leptoperca* Gill)

Two species, *G. schraetser* (Linnaeus), (type species); *G. acerina* (Güldenstädt).

Dorsal spines (16) 17–19; scales in lateral line 54–62; vertebrae 37 to 42; depth of body 18–25: of standard length; snout long, 41–43% of head length; body covered by regular distinct spots arranged in longitudinal rows or by dark longitudinal stripes along the flanks. Exclusively rheophilous.

2) Subgenus *Acerina* Cuvier, 1817 (syn. *Cernua* Fleming)

Two species, *G.* (*A.*) *cernua* (Linnaeus), (type species); *G.* (*A.*) *baloni* sp. n.

Dorsal spines 12–16; scales in lateral line 34–40; vertebrae 32 to 38; depth of body 22–23% of standard length; snout short, 27–

40% of head length; flanks with irregular dark spots or 4–6 transverse bands. Rheophilous (*G. baloni*) or limnophilous or facultatively both (*G. cernua*).

The following discussion of the evolution of the species of *Gymnocephalus* must, of necessity, be speculation, since we have no evidence of evolutionary rates; there is a complete lack of fossil material of earlier than Pleistocene times. All known *Gymnocephalus* remains are from interglacial deposits in Denmark, Germany, Russia, England and Poland (Pawlowska, 1963), and all are *G. cernua*. In our opinion, the subgenus *Acerina* seems to be more specialized than the subgenus *Gymnocephalus*, which exhibits more primitive characters, e.g., more elements in dorsal and anal fins, more scales in lateral line, primitive type of coloration (see Vasnecov, 1934, in this respect) and exclusively rheophilous habits (Fig. 10). Specialization within the genus and within both subgenera was apparently different. For the center of origin and subsequent expansion of the genus *Gymnocephalus*, we assume the Paleodanube sensu Lindberg (1955). From the original rheophilous *Gymnocephalus* stock that lived here arose some rheophilous species similar to the recent *G. schraetser*. From this form, following the severing of the connection between the Dnieper and the Danube, *G. acerina* originated in the basin of the former river and *G. schraetser* in the basin of the latter. In other words, the main speciation factor here was geographic isolation (Fig. 11). On the other hand, some rheophilo-limnophilous form arose later from the original rheophilous *Gymnocephalus* stock and has spread radially, leading to the differentiation of *G. cernua*, and *G. baloni* in the Danube River basin. The very close affinity between *G. cernua* and *G. baloni* suggests relatively late speciation within the subgenus *Acerina*, the main factor of which seems to have been ecological specialisation. Some apparently primitive features of *G. baloni* (serrations of the subopercles, spines on the opercles, more elements in fins and lateral line) suggest that this species is nearer to the original stem than *G. cernua*, whose features are more specialised. These ideas, however, are speculative and require support from both ecology and palaeontology. Unfortunately, there are few ecological data except for *G. cernua*, and, as stated already, fossil material is scarce and relatively recent. This lack of older fossils is surprising and so far has not been explained, as noted by Svetovidov and Dorofeeva (1963). Since the Danube basin is known to be almost without fish fossils, we take this to be indirect support for our view that the Palaeodanube was the center of origin and distribution of the genus *Gymnocephalus*.

Key for the identification of *Gymnocephalus* species:

1 (4) D (XVI) XVII–XX; lateral line 48–65; vertebrae 37–42; snout length 41–53% of head length ..... Subgenus *Gymnocephalus* sensu stricto

2 (3) Flanks with 3–4 dark longitudinal stripes ..... *Gymnocephalus schraetser* (Linnaeus)

3 (2) Flanks with numerous distinct, circular dark spots arranged in more or less regular rows ..... *Gymnocephalus acerina* (Güldenstädt)

4 (1) D XI–XVI; lateral line 35–46; vertebrae 32–38; snout length 27–40% of head length ..... Subgenus *Acerina*

5 (6) Flanks with irregular spots of different size grouped in 4–6 transverse bands; opercle with two distinct spines; distal edge of dorsal fin perpendicular to caudal peduncle line ..... *Gymnocephalus* (*Acerina*) *baloni* sp. n.

6 (5) Flanks with numerous small irregular spots of different size; opercle with one spine; distal edge of dorsal fin oblique ..... *Gymnocephalus* (*Acerina*) *cernua* (Linnaeus)

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ABBREVIATIONS USED

SNM-RY — Slovak National Museum, Ichthyological collection, Bratislava
CU-RY — Comenius University, Ichthyological collection of the Faculty of Sciences, Bratislava
LFRH — Laboratory of Fishery Research and Hydrobiology. Slovak Academy of Agricultural Sciences, Bratislava
ZICU — Zoological Institute of Charles University, Prague
IBTS — Institute of Biology "Traian Savulescu," Bucarest
ZMB — Natural History Museum, Berlin
BMNH — British Museum (Natural History), London
ZSMI — Zoological State Collection (Ichthyology), Munich

Comparative material.—Gymnocephalus cernua (Linnaeus) LFRH 98288, (21), Danube River (backwater Žofín-Vojka), Slovakia; CU-RY 294, (4), canal Čilizská Radvaň-Klúčovec, Slovakia; ZMB 22301, (5), Sweden; ZMB 368, (1), Berlin, Germany; ZMB 4878, (1), Berlin, Germany; ZMB 369, (2), Germany; ZMB 10245, (5), Obdorsk (Ob drainage), USSR; BMNH 1862.12.6:1, (1), Sweden; BMNH 1835.3.16:91–96, (5), Gotha River, Sweden; BMNH 1864.11.9:55–56, (2), Munio River, Sweden: BMNH 1954.10.8:1, (1), Glen River, England; BMNH 1961.4.19:106–115, (6), Thames River near Reading, England.

Specimens seen but not measured: ZICU 18319-328, -339, -342, -343, 348-350, -353, (10), Ženich pond near Třeboň, Bohemia; ZICU 30158, -162, -166-67, -176, -179, -182, 30227, -240, 447, (10), Slapy valley reservoir at Zivohost, Bohemia; LFRH 98289, (3), Danube delta at Ivancea, Roumania; LFRH 98290, (3), Gälätuiu lake, floodplain of Danube River near Călărasi, Roumania; LFRH 98291, (5), Timis River at Peciul Nou, Roumania; ZSMI 18248-57, (10), Danube at Straubing a.d. Donau, Bavaria; ZSMI 2453-2459/49, (7), Danube at Straubing a.d. Donau, Bavaria; ZSMI 789-790/46, (2), Ammersee, Bavaria; ZSMI 1244-1251/48, (8), Danube at Straubing a.d. Donau, Bavaria; ZSMI 510-511/47, (2), Ammersee near Herrsching, Bavaria.

Gymnocephalus cernua × *Gymnocephalus baloni.* CU-RY 42, (11), Danube at Bratislava (Karlova Ves), Slovakia.

Gymnocephalus acerina (Güldenstädt, 1774)). CU-RY/Z 153, (5), Dnieper River near Kanevo, USSR.

Gymnocephalus schraetser (Linnaeus, 1758). LFRH 98282, (4), Danube River (backwater Zofin-Vojka), Slovakia; CU-RY 82, (1), Danube at Radvaň nad Dunajom, Slovakia; CU-RY 277, (3), Danube River at Štúrovo, Slovakia; BMNH 1896-10.3:45, (1), Danube River at Vienna, Austria.

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