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Rodzaj *Coregonus* L. w świetle nowej cechy systematycznej — kształtu i proporcji os maxillare i os supramaxillare

Обзор рода *Coregonus* L. на основании нового систематического признака — формы и пропорции os maxillare и os supramaxillare

Genus *Coregonus* L. discussed in connection with a new systematic feature that of shape and proportion of os maxillare and os supramaxillare

[Pl. XXI — XXXII]

INTRODUCTION

The classification of species and of lower systematic units within the genus *Coregonus* L. is being discussed by numerous authors both in Eurasia and in the North America. The discussion in question can be outlined as follows:

The Soviet investigators headed by BERG (1948) and PRAVDIN (1954) base the division of the Coregonids mainly on morphological features though they refer also to the biotic features and to the ecological forming factors. The morphological tendency prevails in the works of the American authors as well. KOELZ (1929, 1931) enriched considerably the division into species and subspecies but HILE (1938) criticized this splitting and advised analytic and experimental investigations

to be carried on in order to establish and set apart the essential characters that would serve as criteria while establishing the relationships within such a plastic group. DYMOND'S (1943) attitude towards a great number of species described on the area of the USA is also critical; from his point of view these forms are closely related or even conspecific with the Asiatic ones, e.g. *Coregonus clupeaformis* (MITCHILL) is conspecific with the Asiatic *C. nasus* (PALLAS). WYNNE-EDWARDS (1952) states also a close relationship between the American forms and the Asiatic ones and he considers the different forms of *Coregonus* L. in North America as belonging to one universal Holarctic species, *Coregonus lavaretus* (L.). Recently WALTERS (1955) admits the great similarity of all forms of the genus *Coregonus* L. in the whole drainage system of the Arctic Ocean, and, in his opinion, the present classification of this group of fishes ought to be revised.

Among the other investigators one should mention in the first place the Swiss author STEINMANN (1950, 1951). He places the whitefishes of the Alpine lakes in *Coregonus lavaretus* (L.) and he distinguishes among them different ecological forms basing his divisions mainly on biotic differences and on the forming factors of the environment. According to his opinion the Swiss whitefishes populated the lakes in the Postglacial epoch. They originated from one species, the numerous populations of which living in separate biotops of the Alpine lakes have reached by now a degree of differentiation of nationes or ecotypes.

The Swedish author SVÄRDSON (1957) has recently investigated the classification of the Coregonids. He distinguishes in the genus *Coregonus* L. three groups of related species, each group being composed of a certain number of „sibling, partly cryptic species”. He takes into consideration the Coregonids of the whole Palaearctic region and divides them in three groups of species, namely: *lavaretus*-, *albula*-, and *cylindraceus*- group but he gives his particular attention only to the first two groups.

Considering the enormous plasticity of forms within the genus *Coregonus* L. as to their morphological and biotic features, the problem of division of this genus cannot be regarded

as positively solved at the present stage of knowledge. Now, introducing a new taxonomic feature — namely the shape and proportion of os maxillare and supramaxillare — by means of which it will be possible to distinguish the forms within the genus *Coregonus* L. I hope to contribute to deepening the knowledge as to the origin of these forms and to the relationship between them.

SHAPE OF MAXILLARE AND SUPRAMAXILLARE

Maxillare and supramaxillare were taken from the right jaw and owing to this the same specimen of fish could be photographed, according to the accepted method, from the left side. The shape of these bones, as I could see dealing with many specimens of the same form, shows great stability. I took the measurements of the width and length of the two parts of the bones above mentioned by putting on graph paper the outline of these bones taken from the photograph.

While analysing the shape and proportion of maxillare and supramaxillare taken from 16 forms of the genus *Coregonus* L. I distinguished four types of these bones and, according to them, four corresponding groups of species, namely the *albula*-, *lavaretus*-, *leucichthys*-, and *paralavaretus*-group. The first two groups are interpreted here otherwise as by SVÄRDSON.

The maxillare of the *albula*-type has a semilunar shape, it is composed of two parts — the proximal part which is short and cylindrical and ends in a condyle, and the distal part which is flattened and elongate. The proportion of the proximal part to the distal one is expressed as 1 : 5. All along the distal part there stretches a terete swelling which is distinctly seen in *Coregonus albula* (L.); the distal margin of this part is smooth, deprived of carving. The supramaxillare has also a semilunar shape, it is long and narrow, the proportion of the width to the length is expressed as 1 : 4 [Pl. XXI, fig. 1a, b, 2a, b]. I place into the *albula*-group the species: *C. albula* (L.) and *C. sardinella* VAL. As to the American forms it seems to me that to the *albula*-group belong the forms whose lower jaw usually projects beyond the upper.

The maxillare of *lavaretus*-type has a long proximal part, its distal part which is comparatively short constitutes

a flat plate of a somewhat rectangular shape, its hind part is furrowed and so its margin is carved [Pl. XXI, fig. 3a]. The terete swelling is either missing on that part or is very slightly visible. The length proportion of the proximal part to the distal part is expressed as 1 : (0,5—0,9). The supra-maxillare is short and wide, the proportion of the width to the length is expressed as 1 : (2—3) [Pl. XXI, fig. 3b]. I place among the *lavaretus*-group: *Coregonus lavaretus* (L.) as interpreted by BERG (1948), *C. muksun* (PALLAS) and from the American forms — *C. clupeaformis* (MITCHILL).

The *leucichthys*-type of the maxillare and supramaxillare is an intermediate between the *albula*-type and the *lavaretus*-type, and the structure of these bones shows a gradual change of shape [Pl. XXII—XXIII]. I place six species in the *leucichthys*-group; four of them, namely *C. autumnalis* (PALLAS), *C. artedi* (LE SUEUR), *C. tugun* (PALLAS) and *C. peled* (GMELIN) have the maxillare similar to that of the *albula*-type [Pl. XXII, fig. 4a, 5a, 6a, Pl. XXIII, fig. 7a] but I must add that in *C. peled* (GMELIN) a slight carving is noticeable at the hind margin similar to that observed in the *lavaretus*-type. The two other species, namely *C. migratorius* (GEORGI) and *C. ussuriensis* BERG, have a maxillare with a slightly carved hind margin, thus more similar to the *lavaretus*-type [Pl. XXIII, fig. 8a, 9a]. The difference in shape of supramaxillare is even greater and the two varieties of shape are more distinct. In the first four species above mentioned the shape of supramaxillare is very similar to that of the *albula*-type [Pl. XXII, fig. 4b, 5b, 6b; Pl. XXIII, fig. 7b]. The proportion of the width to the length is expressed as 1 : 3,2 whereas in the two other species the shape of supramaxillare is similar to that of the *lavaretus*-type and the proportion of its width to its length is expressed as 1 : 2,9 in *C. migratorius* (GEORGI) and as 1 : 2 in *C. ussuriensis* BERG [Pl. XXIII, fig. 8b, 9b].

The chief characteristics of the maxillare of the *paralavaretus*-type are its small dimensions and its extension in width. Only one species belongs to it, namely *C. nasus* (PALLAS) [Pl. XXIV].

I place the four above mentioned groups of Coregonids in the subfamily *Coregoninae* of the family *Salmonidae*, according to the division introduced by REGAN (1914) and accepted by BERG (1940) and by the majority of contemporary investigators of this group of fish.

The tendency to distinguish in the subfamily *Coregoninae* beside the genus *Coregonus* L. also the genus *Prosopium* MILNER¹ with the species *P. cylindraceus* (PALLAS et PENNANT) in Siberia and *P. culteri* EIGENMANN et EIGENMANN in North America is coming ever more distinctly into view. The opposite features which are characteristic for these two genera are given in consideration in the following synopsis of the subfamily *Coregoninae*.

A SYNOPSIS OF THE *COREGONINAE*

- A₁ Nostrils with two flaps, a front and a back one. Body laterally compressed. Young individuals have a silvery body without dark spots. Vestigial teeth in the intermaxillaries and tongue genus *Coregonus* L.
- a₁ Upper mouth opening. Upper jaw extending beyond the front margin of the eye *albula*-group
1. The predorsal length more than 42% of the whole length of the fish (measured from tip of snout to the end of the middle rays of the caudal fin). Lake form on many lakes of the Baltic basin, also in some lakes of the White Sea drainage *Coregonus albula* (L.)
 2. The predorsal length less than 42% of the whole length of the fish (measured from tip of snout to the end of the middle rays of the caudal fin). A migratory river form. From the Kara River (Europe) eastward to the Kolyma River (Asia) *Coregonus sardinella* VAL.
- a₂ Terminal mouth opening. Upper jaw extending beyond the front margin of the eye *leucichthys*-group
- α₁ Supramaxillare of the *albula*-type
 1. Wandering form, from the coastal waters of the Arctic Ocean. It enters all rivers from the Mezen

¹ Genus *Prosopium* MILNER will not be discussed in this paper because of a lack of material.

- River (Europe) up to the Kolyma River (East Siberia) and in America up to the Mackenzie River. It does not enter the River Ob but lives in the Ob Bay and goes for spawning to the local rivers. Gill rakers 35 — 51. Lateral line scales 61 — 68 *Coregonus autumnalis* (PALLAS)
2. River form that never enters the sea. In Arctic Ocean drainage from the Ob River to the Khatanga River (East Siberia). Gill rakers 26 — 33. Lateral line scales 61 — 76 *Coregonus tugun* (PALLAS)
3. River and lake forms, in the Ob Bay a wandering form. Gill rakers 46 — 68. Lateral line scales 76 — 104. *Coregonus peled* (GMELIN)
4. Lake and river forms in North America. Gill rakers 34 — 59. Lateral line scales 66 — 85 *Coregonus artedi* (LE SUEUR)
- α_2 Supramaxillare of the *lavaretus*-type.
1. Lives in the Baikal Lake, enters rivers for spawning. Gill rakers 47 — 51. Lateral line scales 91 — 98. *Coregonus migratorius* (GEORGI)
2. River and lake form. Lives in the Amur River, in the Khanka Lake and in the coastal waters of the southern part of the Okhotsk Sea. Gill rakers 26 — 30. Lateral line scales 86 — 92. *Coregonus ussuriensis* (BERG)
- α_3 Lower mouth opening. Upper jaw not extending the front margin of the eye.
- α_1 Maxillare and supramaxillare of the *lavaretus* -type, the maxillare narrow and long, 3,4 — 4,5 times longer than wide. The length of the lower jaw is bigger or smaller than the smallest height of the body, sometimes it is equal to it. Gill rakers 14 — 72. Numerous, chiefly wandering forms living in rivers and lakes, widespread in the whole Palaearctic and Nearctic regions *lavaretus*-group
1. Length of the lower jaw in general bigger than the smallest height of the body, but there occur individuals whose lower jaw equals the smallest height of the body. Spawning chiefly late in autumn but there are forms that spawn in spring and summer. Gill rakers 14 — 68. Many forms living in the drainage system of the Northern Sea, the Baltic Sea, the White Sea, in the Central European Alpine lakes, in Asia in the Baikal Lake, in the

drainage of the Lena River and in the lakes of Baunt region *Coregonus lavaretus* (L.)

2. Length of the lower jaw in general smaller than the smallest height of the body. Many forms living in rivers, lakes and coastal waters. Widespread in the drainage of the Arctic Ocean, in Eurasia from Murman Peninsula up to the farthest border of north-east Siberia, dominating forms in America. Gill rakers 16 — 72. Lateral line scales 71 — 97 *Coregonus pidschian* (GMELIN)

Snout plate (intermaxillaria) 1,5 times higher than wide. Gill rakers 23 — 24. Living in the drainage of the river Shilka and Argun, partly in Amur . . . *Coregonus pidschian chadary* DYBOWSKI

Chiefly a wandering form, from the brackish waters of the Arctic Ocean enters the Siberian rivers from the Kara River up to the Kolyma River. Gill rakers 44 — 61. There is also a lake form living in the group of the Norylsk Lakes in the drainage of the Piasina River. Gill rakers 45 — 72. Lateral line scales 85 — 97

. *Coregonus pidschian muksun* (PALLAS)

Freshwater and coastal water form living in the Hudson Bay, along the Arctic coast of Canada, south to New York and Michigan, in the inland lakes of Canada and USA. Gill rakers 22 — 33

. *Coregonus pidschian clupeiformis* (MITCHELL)

- σ_2 Maxillare of the *paralavaretus*-type, its width is 2,4 times in the length. The length of the lower jaw is smaller than the smallest height of the body *paralavaretus*-group

Lake and river form living in the drainage of the Arctic Ocean from the Pechora River up to the Kolyma River and farther on the East, stays chiefly in the lower part of rivers. Gill rakers 19 — 27. Lateral line scales 85 — 106

. *Coregonus nasus* (PALLAS)

- A₂ Only one flap between the nostrils. Body subterete. Young individuals with dark spots on the back. No teeth genus *Prosopium* MILNER.

¹ I examined the material of Canada received from Dr. V. VLADYKOV, and some specimens in the collection of Professor Dr. F. STAFF, the exact water body of these specimens which were imported from North America was not known.

SOME HISTORICAL REMARKS ON THE INVESTIGATIONS OF
COREGONUS LAVARETUS L.

Coregonus lavaretus L. was described by LINNÉ, 1758, as *Salmo lavaretus* L. This description was based on the European material. The great plasticity of whitefish inspired the investigators of the post-Linnéan period to describe numerous other species. But since the beginning of the 20th century the analytical works dealing with the differences and similarities of European whitefish made it possible to revise the far reaching division of the genus *Coregonus* L. into species. COLLET (1903), THIENEMANN (1922, 1928), KULMATYCKI (1926—1927) and BERG (1932) expressed the opinion that such species as *C. oxyrhynchus* (L.), *C. generosus* PETERS, *C. wartmanni* BLOCH, *C. fera* JURINE and others should be considered as varieties of *C. lavaretus* (L.).

BERG (1948) after summing up numerous opinions of his predecessors as well as his own concerning *Coregonus lavaretus* (L.), interpreted this species more widely and included to it many forms that differ not only by the number of gill rakers which should vary from 15 to 60, but by other features as well. He places here the whitefish of the North Sea drainage, of the Baltic Sea, the White Sea, the Arctic Ocean, as well as of the Alpine lakes and of the Baikal Lake. BERG has based his system mainly on morphological features but taking into consideration also the ecological features and partly the biotic characters. He states namely that forms belonging to these species multiply late in the autumn or early in the winter, but he quotes a case of a very ripe female that was caught on 5 IV 1935 in the Bothnian Gulf near the Finnish town Vaasa. Our knowledge as to the time of spawning was considerably enriched by STEINMANN (1950) who wrote about the Alpine whitefish as follows: „Im allgemeinen gelten die Koregonen als Winterlaicher.“ — „Der Edelfisch des Vierwaldstättersees laicht am Juli bis in den September hinein, der Kropfer und Brienzling des Thunersees und der Brienersees kam im Spätsommer zum Laich, und das gleiche gilt von gewissen Laichschwärmen des Vierwaldstättersees und des Walensees („Sommeralbeli“).“ *C. lavaretus baunti* (MUCHOMEDIAROV) is the form that spawns in the spring; it lives in the group of the Baunt

Lakes in the drainage of the Lena River (ANPILOVA, 1956). A very ripe female was caught in the Leba Lake on the Polish Baltic coast on the 13th April 1958 (Mr. S. KOSMULSKI, in litt.).

SVÄRDSON (1957) places in the *lavaretus*-group the following five species: *C. pidschian* (GMELIN), *C. nasus* (PALLAS), *C. lavaretus* (L.), *C. oxyrhynchus* (L.) and *C. peled* (GMELIN). He gives the following reasons for placing them together (page 274): „This is an opinion based first on the rule that two sympatric populations must belong to different species and, secondly, on the principle that the genetic morphological character of the species is mainly the number of gillrakers“.

When using the new features in the classification of the genus *Coregonus* L., one cannot agree with SVÄRDSON as to his concept of the *lavaretus*-group. First of all, *C. peled* (GMELIN) differs from the other species of this group by such essential features as the position of the mouth opening, the extension of the upper jaw beyond the margin of the eye [Pl. XXIX, fig. 28] and the shape and proportion of maxillare and supra-maxillare [Pl. XXII, fig. 6a, b]. Secondly, SVÄRDSON puts into the synonyms of *C. lavaretus* (L.) the following forms: *C. wartmanni* (BLOCH), *C. maraena* (BLOCH), *C. tugun* (PALLAS) and *C. ussuriensis* BERG. I confront the forms in question in the table given on the page 10.

From the above given comparison of characters we can see that there is only one common to all three forms, namely the number of gill rakers; the other features are different. For this reason it is impossible to consider these names as synonyms and regard these forms as conspecific.

A fuller consideration should be given also to the dwarfed form of *C. lavaretus* (L.) which according to SVÄRDSON (1957) lives in the Swedish lakes together with the other forms of whitefish. SVÄRDSON (pag. 279) says thereabout: „It is often strong dwarfed, 10–20 cm, and lives in running water“. — „When some specimens of *C. tugun* from Jenissei were inspected at the Museum of Natural History in Stockholm it was quite evident that *tugun* was no cisco but a dwarfed whitefish, just as *lavaretus* was often known to be“. The dwarfed form living in the Swedish lakes seems to be either the proper form of *C. tugun* (PALLAS), which can be verified by examining

its maxillare and supramaxillare, or a hybrid of whitefish \times small whitefish which is suggested by the following remark made by SVÄRDSON (1957, page 279): „in the smaller lakes,

Features	<i>C. lavaretus maraena</i> (BLOCH.)	<i>C. tugun</i> (PALLAS)	<i>C. ussuriensis</i> BERG
position of mouth opening	lower	terminal	terminal
length of upper jaw	does not reach the front margin of the eye	reaches beyond the front margin of the eye	reaches beyond the front margin of the eye
maxillare	lavaretus-type	albula-type	leucichthys-type
supramaxillare	lavaretus-type	albula-type	lavaretus-type
maxillare proximal part: distal part	1 : 2,0	1 : 2,7	1 : 2,3
number of gill rakers	29—34	26—33	26—30
lateral line scales	—	61—76	86—92
consistency of scales	hard, strong fitted to the skin	soft, easily falls off	—

especially the colder ones in the higher altitudes, *lavaretus* looks more and more like cisco. The nose is very much shortened in these small fish, but they never have pronounced antrorse premaxillaries, as the true ciscoes have“. The hybrids of whitefish \times small whitefish which I got by way of artificial fertilization had intermediate external features in comparison with the parental specimens (GAŠOWSKA, 1958).

One cannot agree with SVÄRDSON either when he considers *C. oxyrhynchus* (L.) as a separate species. As to this form [Pl. XXXI, fig. 36], the number of gill rakers (36—44) and the shape of maxillare and supramaxillare (Pl. XXVI, fig. 16a, b) correspond exactly to the diagnosis of *C. lavaretus* (L.). THIENEMANN (1922) stated a series of intermediate forms of *C. oxyrhynchus* (L.) from a form with a slightly elongate snout to a form with a very elongate one, pointed at the end. THIENEMANN (1922, p. 444) summed up his point of view on *C. lavaretus oxyrhynchus* (L.) as follows: "Die verschiedenen *Oxyrhynchus*-Formen bilden sicher keine einheitliche, genetisch zusammenhängende Entwicklungsreihe, so daß etwa der Vänern- und Vätternschnäpel die Stammform des Schleischnäpels und dieser wiederum die Stammform des Nordseeschnäpels sei. Dagegen spricht außer der räumlichen Trennung dieser Formen schon die qualitativ verschiedene Gestaltung ihrer Nasen. Vielmehr stellt der *Oxyrhynchus*-Typus der *Lavaretus*-Art eine Konvergenzerscheinung dar. Die hier als *Lavaretus oxyrhynchus* zusammengefaßten *Coregonen*kolonien sind aus der gemeinsamen *Lavaretus*-Stammform selbstständig an verschiedenen Stellen entstanden".

Basing his division of the *lavaretus*-group on the number of gill rakers, SVÄRDSON (1957) considers *C. autumnalis* (PALLAS) having 40-42 gill rakers and *C. migratorius* (GEORGI) having 47—51 gill rakers as synonyms of *C. oxyrhynchus* (L.) having 36—44 gill rakers. One cannot agree with him and his division if one compares the shape of maxillare and supramaxillare of the last species [Pl. XXII, fig. 4a, b] with the shape of the same bones of the two other [Pl. XXIII, fig. 8a, b; Pl. XXVI, fig. 16a, b]. The position of the mouth contradicts also the identification of these three forms [Pl. XXIX, fig. 25, 29; Pl. XXXI, fig. 36].

GILL RAKERS AS A SYSTEMATIC FEATURE IN *COREGONUS LAVARETUS* (L.)

The number of gill rakers which SVÄRDSON considers as a basic feature of the specific value has, in my opinion, a rather limited importance. It is distinctly seen when one takes into consideration another feature which is also hereditary,

namely the schooling behaviour of whitefish. STEINMANN (1950, p. 146) discussed this property of whitefish: „Die Neigung der Schwärmebildung ist dieser Salmonidengattung tief einverwurzelt und zeigt sich schon außerordentlich früh in den Brutstadien“. — „Hier sei nur festgehalten, daß die Koregonen bei ihrer kollektiven Wanderungen bestimmte Wanderungen einschlagen, die für die einzelnen Sippen verschieden sind, und daß, soweit man das heute beurteilen kann, ein merkwürdiges Ortgedächtnis besteht, das die einzelnen Fischschwärme an bestimmte, ihnen offenbar seit Generationen eigene Laichorte, führt“. The same was stressed by LINDROTH (1957, p. 86) who says: „no specimen of *C. lavaretus* from Indalsälven was ever recaptured in any other river“. — „not even from Ljungan which empties into the same bay“. The distance between the mouths of these two rivers amounts to about 10 kilometers (author's remark).

The inclination of whitefish to keep to a group may be caused ever by the mechanical joining, according to the observations made by KENNEDY (1954) on tagged individuals of *C. clupeaformis* (MITCHILL) from the Winnipeg Lake. When tagged fish were put into the lake during one day or during two days in succession, they were, later on, caught together. One couple kept together for five years. When tagged whitefish were put into the water in different places they also formed several distinct „schools“ and did not join into a single one. This inclination of whitefish to live in isolated groups accustomed to the chosen places and biotops results in the well known differentiation of genus *Coregonus* L. and particularly of the *lavaretus*-group. I should like to quote the example of the forms of whitefish living in the Ladoga Lake; they live their own life in certain definite areas of this big lake and spawn always in the same place. *C. lavaretus lavaretus* typ. (POLJAKOV), with 27—37 gill rakers, lives mainly in the north-east part of the lake, for spawning enters the Vodla River; *C. lavaretus lavaretoides* n. *schuensis* PRAVDIN, with 30—37 gill rakers, is spread all over the lake and spawns in the upper part of the Shuya River. Speaking of these numerous forms of whitefishes PRAVDIN (1955) says as follows: „In the Ladoga Lake there live about seven groups of whitefishes,

they all belong to one species *Coregonus lavaretus* (L.) but differ morphologically and biologically. All these seven groups are only separate populations of the species above mentioned having a definite structure, they are infraspecific units which should be considered as a manifestation of an everlasting evolution of this exceedingly polymorphic species". The same opinion was expressed even much earlier by FREIDENFELT (1934) with regard to the whitefish of the Vänern Lake; on page 59 he says: „Die natürlichen Gruppen, mit denen wir hier zu tun haben, sind die lokalen „Rassen“, d. h. die Gruppen von Individuen, die dieselben Lebensweise führen und vor allen Dingen ihr Laichen zur gleichen Zeit und an gleicher Stelle verrichten“.

The number of gill rakers is no doubt a feature genetically fixed but as a taxonomic feature it is important only by the differentiation of smaller taxonomic units, namely infraspecific forms. At the same time, the biotic features should be taken into consideration. Since whitefish keeps together in school and wanders together to customary places for spawning a constant number of gill rakers prevails in every particular population. In this matter it is difficult to agree with SVÄRDSON (1957) and with LINDROTH (1957) who differentiate two species among the whitefishes living in the Sundvall Bay, namely: *C. lavaretus* (L.), with 26—37 (31,04) gill rakers, a wandering whitefish that enters the Indalsälven River for spawning, and *C. nasus* (PALLAS), with 24—33 (27,48) gill rakers, which does not leave the bay and spawns near the banks of the local island Alnö.

This „*Coregonus nasus* (PALLAS)“ which SVÄRDSON considers to be a synonym of *C. lavaretus* f. *polonica* KULMATYCKI, 1926, should be also discussed. Dr. G. SVÄRDSON kindly sent me several specimens from Sweden, identified as „*C. nasus* (PALLAS)“ enabling me to compare this form with the form described by KULMATYCKI¹. I should like to express here my heartiest thanks to dr. SVÄRDSON for his efficient help.

¹ Specimens of *C. lavaretus* f. *polonica* KULMATYCKI, 1926, from KULMATYCKI's collection are kept in the collection of the Institute of Zoology of the Polish Academy of Sciences in Warszawa.

After the shape of the jaw bones *C. lavaretus* f. *polonica* KULMATYCKI belongs to the *lavaretus*-group and after the number of gill rakers (20—21 in the average) and its biotic features it belongs to *C. lavaretus lavaretus* (L.) which is a wandering, coastal form of the Baltic Sea (Pl. XXV, fig. 11a,b; 12a,b).

As to the "*C. nasus* (PALLAS)", sensu SVÄRDSON, 1957, this form having 23—34 gill rakers in the average, the shape of the jaw bones of the *lavaretus*-type and the length of the lower jaw bigger than the smallest height of the body¹, it also belongs to *C. lavaretus lavaretus* (L.), in spite of the somewhat elongated snout [Pl. XXV, fig. 11a, b; 13a, b; Pl. XXIX, fig. 31, 33]. It cannot be identified with the proper *C. nasus* (PALLAS) from the Arctic Ocean drainage because the shape of jaw bones is different as well as the length of the lower jaw, being in *C. nasus* (PALLAS) smaller than the smallest height of the body. These differences are reasons why I put the last form into a separate *paralavaretus*-group [Pl. XXIV].

One cannot agree also with SVÄRDSON when he synonymizes *C. peled* (PALLAS), 46—68 gill rakers, with *C. generosus* (PETERS), 38—46 gill rakers, and *C. muksun* (PALLAS), 44—72 gill rakers, only on the base of similar number of gill rakers. While comparing these three forms we must state the differences in the shape of maxillare and supramaxillare [Pl. XXII, fig. 6a, b; Pl. XXV, fig. 14a, b; Pl. XXVII, fig. 21a, b] as well as in the position of the mouth opening and the extent of the upper jaw in relation to the eye [Pl. XXIX, fig. 28; Pl. XXX, fig. 34; Pl. XXXII, fig. 41].

DISCUSSION

The analysis of the genus *Coregonus* L. suggests the following remarks:

An investigator, while recognizing species should make use of the morphological as well as of the ecological, physiological, biotic and genetic criteria. The prevalence of one or other of these criteria depends on the category of the syste-

¹ The measurements are performed by the author herself.

matic units is being considered, namely — infraspecific or supraspecific one. A systematist starts traditionally with the morphological features but the degree of their constancy can be distinctly seen only when the biology and ecology of the species are studied. According to the biological conception „species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups“ (MAYR, 1947, p.120). The biological approach to the species should be used as a control of its morphological statement which is only a preliminary stage of a taxonomic diagnosis. In the present stage of our knowledge of species of *Coregonus* L. their morphological and anatomic features are the most constant ones, and it also proves their shaping role of the ecological factors.

The main biological feature of species namely their reproductive isolation, is but little fixed in the *lavaretus*-group. STEINMANN (1950), SVÄRDSON (1957) and LINDROTH (1957) state the lack of a complete barrier for interbreeding between sympatric species and, consequently, limits of populations living sympatrically, if based on this feature, are rather problematic. These populations would be nothing more than infraspecific units of one or another category. For instance, the facility of the intercrossing of forms living sympatrically in the Swedish lakes contradicts the statement as if they were good species.

Within the genus *Coregonus* L. even forms with great morphological and ecological distinctions, such as: *C. albula* (L.) and *C. lavaretus* (L.), when artificially crossed, give completely normal offspring of the F₁ generation which grow to mature individuals with the normal numerical relationship of both sexes. The author got individuals of F₂ generation that were sexually mature (GAŚOWSKA, 1957). Interspecific hybrids are also known to occur rather frequently in natural conditions, e. g. *C. autumnalis* (PALLAS) × *C. lavaretus* n. *juca-giricus* DRJAGIN, as BERG (1948) quotes it after N. A. OSTROMOV. The above given opinion proves that even different species of the genus *Coregonus* L. give normal and fertile offspring which testifies that these species are still young and their reproductive isolation is not yet completely fixed.

One cannot agree with SVÄRDSON and consider the sympatric forms populating inland and coastal waters in the drainage of the Baltic Sea — sometimes as many as three species in one lake — as forms that arose allopatrically through geographical isolation and as such arrived from East-North Europe in the Glacial and Postglacial epoch. *C. lavaretus* infraspecies *oxyrhynchus* (L.)¹ may serve as an example of postglacial, local differentiation of *C. lavaretus* (L.). This infraspecies shows great variability as to the length of the snout. Its form named „Nordseeschnäpel“ has the most elongate snout; it is a wandering form, living in the farthest western area along the southern banks of the North Sea. The form named „Schleischnäpel“ has a less elongate and pointed snout; it lives in the Schlei River that enters the Baltic Sea. The same can be said about the whitefish of the Swedish lakes. The form *oxyrhynchus* (L.) is not found farther to the West, it is not known on the British Islands and east to the Baltic Sea drainage. Only in the upper and middle part of the Jenissei River in Siberia and in its affluents a form with a considerably elongate and blunt snout is found; it is named *C. lavaretus pidschian natio fluviatilis* ISSATCHENKO and has 18—23 gill rakers. This fact proves that in certain specific conditions there may arise quite independently a local form with a characteristically elongate snout. One should notice that in the Polish Mazurian lakes we find, besides the whitefish with a blunt cut snout, another form with a conic snout (GAŠOWSKA, 1953). BERG (1948) states that these two forms live side by side also in the Peipus Lake. The above mentioned facts indicate that the form *oxyrhynchus* has originated from one of the forms living in the Baltic Sea which in its historical development was more widely bound with the North Sea.

Investigators will have to make many efforts before they are able to put the forms of the genus *Coregonus* L. in a more fixed taxonomic frame. The keen papers that we have had up till now which consider this systematic problem from different point of view such as genetics, biology, ecology and morphology, bring a lot of valuable information but, on the other hand,

¹ The name of the form cited after BERG (1948).

they sometimes come to contradictory conclusions. It means that this branch of knowledge has not yet found proper solutions.

It would be very helpful in solving the problem of relationship and in determining the infraspecific units if an uniform method of investigations was accepted. This method should consider the morphology as well as the biology and anatomy of the investigated populations and the character of environment which conspicuously shapes the organism.

A widespread application of experimental breeding of different forms in similar conditions of environment, for example in experimental ponds, can be very helpful in determining the degree of constancy of morphological and biotic features.

Tagging, as one of the experimental methods, should be applied commonly.

The acclimatization and crossing of systematically distinct forms may be very helpful in finding their intergrades.

The above presented attempt to solve this problem on the ground of the shape and proportion of maxillare and supra-maxillare should be proved by further investigations. It is very important to examine the shape of these bones in correlation with the proportion of the length of the lower jaw to the smallest height of the body. The material I had at my disposal was rather limited.

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Humboldt University, Berlin; Dr E. DOTTRENS — Director of the Museum of Natural History, Genève.

LITERATURE

- ANPILOVA V. I. 1956. O sistematičeskom položennii bauntovskoj rjapuški. Dokl. Akad. Nauk. SSSR. Leningrad—Moskva, **111**: 898—900.
- BERG L. S. 1932 (1948). Ryby presnych vod SSSR i sopredelnyh stran. Moskva.
- BERG L. S. 1940. Classification of Fishes, both recent and fossil. Trav. Inst. Zool. Acad. Sci. URSS, Leningrad, **5**: 346—517.
- DAHR E. 1947. Biologiska studier över siken *Coregonus lavaretus* LINNÉ vid mellansvenska östersjökusten. Rep. Swed. Stat. Institut. Freshwater Res., Drottningholm, **28**: 71—75.
- DYMOND J. R. 1943. The Coregonine Fishes of Northwestern Canada. Trans. Royal Canadian Institute, Toronto, **24**, part 2, 172—232.
- ESCHMAYR P. H. and BAILEY R. M. 1955. The pygmy Whitefish, *Coregonus coulteri* in Lake Superior. Trans. Amer. Fish. Soc., New York, **84**: 161—199.
- FREIDENFELT T. 1934. Untersuchungen über die Coregonen des Wenersees. Int. Rev. Hydrobiol., Leipzig, **30**: 49—163.
- GĄSOWSKA M. 1953. Sieja jezior mazurskich. Roczn. Nauk. Roln., Warszawa, **67-B-1**.
- GĄSOWSKA M. 1957. Drugie pokolenie krzyżówki po rodzicach samiec sieja i samica sielawa. Gospodarka Rybna, Warszawa, **9**.
- GĄSOWSKA M. 1958. The morphology of hybrids and ways of inheriting parental features by reciprocal hybrids: whitefish x small whitefish (*Coregonus lavaretus maraenoides* POLJAKOV x *C. albula* (L.)), Pol. Arch. Hydrob., Warszawa, **4**: 277—287.
- HILE R. 1938. Morphometry of the cisco, *Leucichthys artedi* (LE SUEUR), in the lakes of the Northeastern Highlands. Wisconsin. Intern. Rev. **36**: 57—130.
- KAJ J. 1955. Sieja jezior Miedzzychodzkiech. Wyd. Mat.-Przyt., Praco Kom. N. Roln. Leś., Poznań, **2** (9): 4—75.
- KENNEDY W. A. 1954. Tagging returns, age studies and fluctuations in abundance of Lake Winnipeg whitefish, 1931—1951. Journ. Fish. Res. Board of Canada, Ottawa, **11** (3): 284—309.
- KOELZ W. 1929. Coregonid Fishes of the Great Lakes. Bull. U. S. Bur. Fish., Washington, **43** (2): 297—643.
- KOELZ W. 1931. The Coregonid Fishes of Northeastern America. Pap. Mich. Acad. Sci. Arts and Letters, Ann Arbor, **13**: 303—432.
- KULMATYCKI W. 1926—1927. Studien an Coregonen Polens. Arch. Hydrobiol. Ryb., Suwalki, **1—2**: 275—336, 1—40.

- LINDROTH A. 1957. A study of the whitefish (*Coregonus*) of the Sundsvall Bay District. Rep. Inst. Freshwater Res., Drottningholm, **38**: 70—108.
- MAYR E. 1947. Systematics and the origin of species. New York.
- PRAVDIN J. F. 1954. Sigi vodojomov Karelo-Finskoj SSR. Akad. Nauk SSSR. Moskva.
- REDEKE H. C. 1934. Über der Rheinschnäpel, *Coregonus oxyrhynchus* L., Verh. intern. Ver. theor. Limnol. Stuttgart, **6**: 352—357.
- REGAN C. T. 1914. The systematic arrangement of the fishes of the family *Salmonidae*. Ann. Mag. Nat. Hist. London, **13**: 405—408.
- STEINMANN P. 1948. Der Weißfelchen des Bodensees und die Frage der Artbildung im Felchengeschlecht. Schweiz. Zeitschr. Hydrol., **10**: 3—12.
- STEINMANN P. 1950—51. Monographie der Schweizerischen Koregonen. Beitrag zum Problem der Entstehung neuer Arten. Schweiz. Zeitschr. Hydrol., **12**: 109—189, 340—491.
- STEINMANN P. 1951. Monographie der schweizerischen Koregonen. *ibid.* **13**: 54—155.
- STEINMANN P. 1950. Ein neues System der mitteleuropäischen Coregonen. Rev. suisse zool., Genève, **57**: 517—525.
- SVÄRDSON G. 1952. The Coregonid Problem. IV. The significance of scales and gillrakers. Rep. Inst. Freshw. Res., Drottningholm, **33**: 204—232.
- SVÄRDSON G. 1953. The Coregonid Problem. V. Sympatric whitefish species of the Lake Idsjön, Storsjön and Hornavan. *ibid.* **34**: 141—166.
- SVÄRDSON G. 1957. The Coregonid Problem. VI. The Palearctic species and their intergrades. *ibid.* **38**: 267—356.
- THIENEMANN A. 1922. Weitere Untersuchungen an Coregonen. Arch. Hydrob., Stuttgart, **13**: 415—475.
- THIENEMANN A. 1928. Über die Edelmaräne (*Coregonus lavaretus* forma *generosus* PETERS) und die von ihr bewohnten Seen. Arch. Hydrobiol., Stuttgart, **19**: 1—36.
- WALTERS V. 1955. Fishes of Western Arctic America and Eastern Arctic Siberia. Bull. Amer. Nat. Hist., New York, **106**: 255—368.
- WYNNE-EDWARDS V. C. 1952. Freshwater Vertebrates of the Arctic and Subarctic. Bull. Fish. Res. Board Canada, Ottawa, **94**: 10—16.

STRESZCZENIE

Autorka wprowadza do systematyki rodzaju *Coregonus* L. nową cechę rozpoznawczą, mianowicie kształt i proporcje maxillare i supramaxillare, stwierdziwszy różnicowanie tej cechy na materiale 16 form pochodzących z różnych miejsc

Europy, Azji i Ameryki Północnej. Autorka dowodzi, że liczba wyrostków filtracyjnych, uważana przez niektórych badaczy za najważniejszą cechę gatunkową, ma podrzędną wartość taksonomiczną i może być wykorzystywana jedynie do celów systematyki wewnątrzgatunkowej. Praca stanowi wstępną rewizję rodzaju *Coregonus* L. w oparciu o nowo wprowadzoną cechę.

РЕЗЮМЕ

Автор вводит в систематику рода *Coregonus* L. новый признак, а именно форму и пропорцию maxillare и supra-maxillare. Дифференциация этого признака была проверена автором на материале 16 форм из разных водоемов Европы, Азии и Северной Америки. Автор доказывает, что число жаберных тычинок, признаваемое некоторыми авторами как наиболее надежный признак для распознавания отдельных видов рода *Coregonus* L., имеет второстепенное таксономическое значение. Оно может быть использовано только для целей внутривидовой систематики. Эта работа является предварительной ревизией рода *Coregonus* L. на базе нового признака.

Plate XXI

a — maxillare; b — supramaxillare

Fig. 1. *Coregonus albula* (L.), Wdzydze Lake, Poland.

Fig. 2. *Coregonus sardinella* VAL., Sibircha River, European Russia.

Fig. 3. *Coregonus lavaretus* (L.), Goldopiwo Lake, Poland.

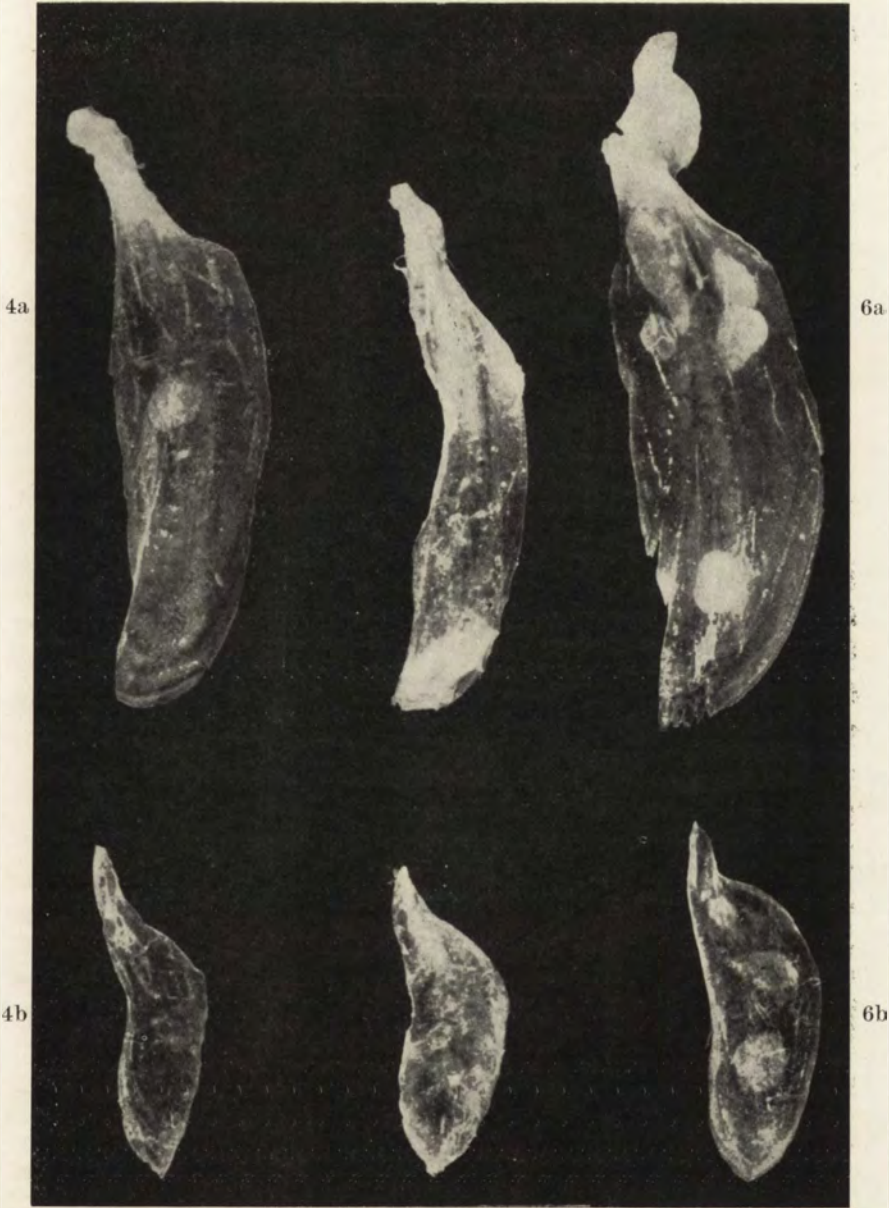


J. Stefaniak phot.
M. Gąsowska

Plate XXII

- a — maxillare; b — supramaxillare of the *leucichthys*-group
Fig. 4. *Coregonus autumnalis* (PALLAS), Yugorski Shar Strait, USSR.
Fig. 5. *Coregonus artedi* (Le SUEUR), Lake Superior, N. America.
Fig. 6. *Coregonus peled* (GMELIN), Andermei Lake, drainage of the
Kara River, USSR.

5a



J. Stefaniak phot.
M. Gąsowska

5b

Plate XXIII

a — maxillare; b — supramaxillare of the *leucichthys*-group.

Fig. 7. *Coregonus tugun* (PALLAS), det. PRAVDIN.

Fig. 8. *Coregonus migratorius* (GEORGI), Baikal Lake.

Fig. 9. *Coregonus ussuriensis* BERG, Amur River.



J. Stefaniak phot.

M. Gąsowska

8b

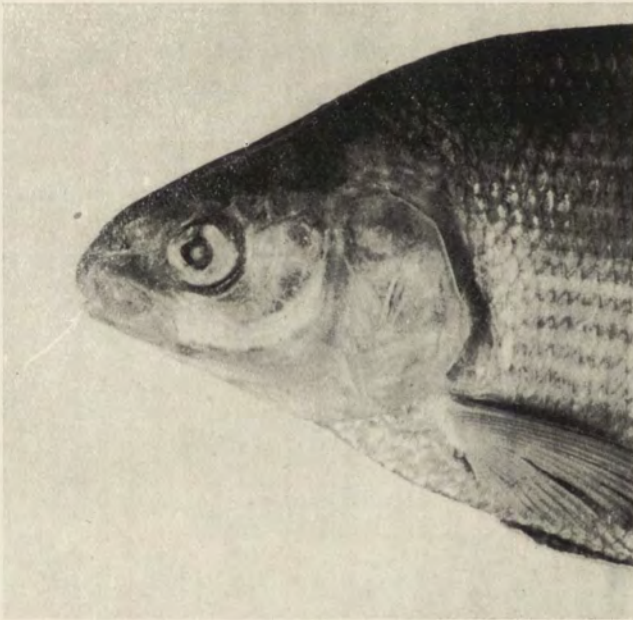
Plate XXIV

Fig. 10. *Coregonus nasus* (PALLAS), mouth of the Ob River; a — maxillare, b — supramaxillare, c — head.

10a



10b



10c

J. Stefaniak phot.
M. Gąsowska

Plate XXV

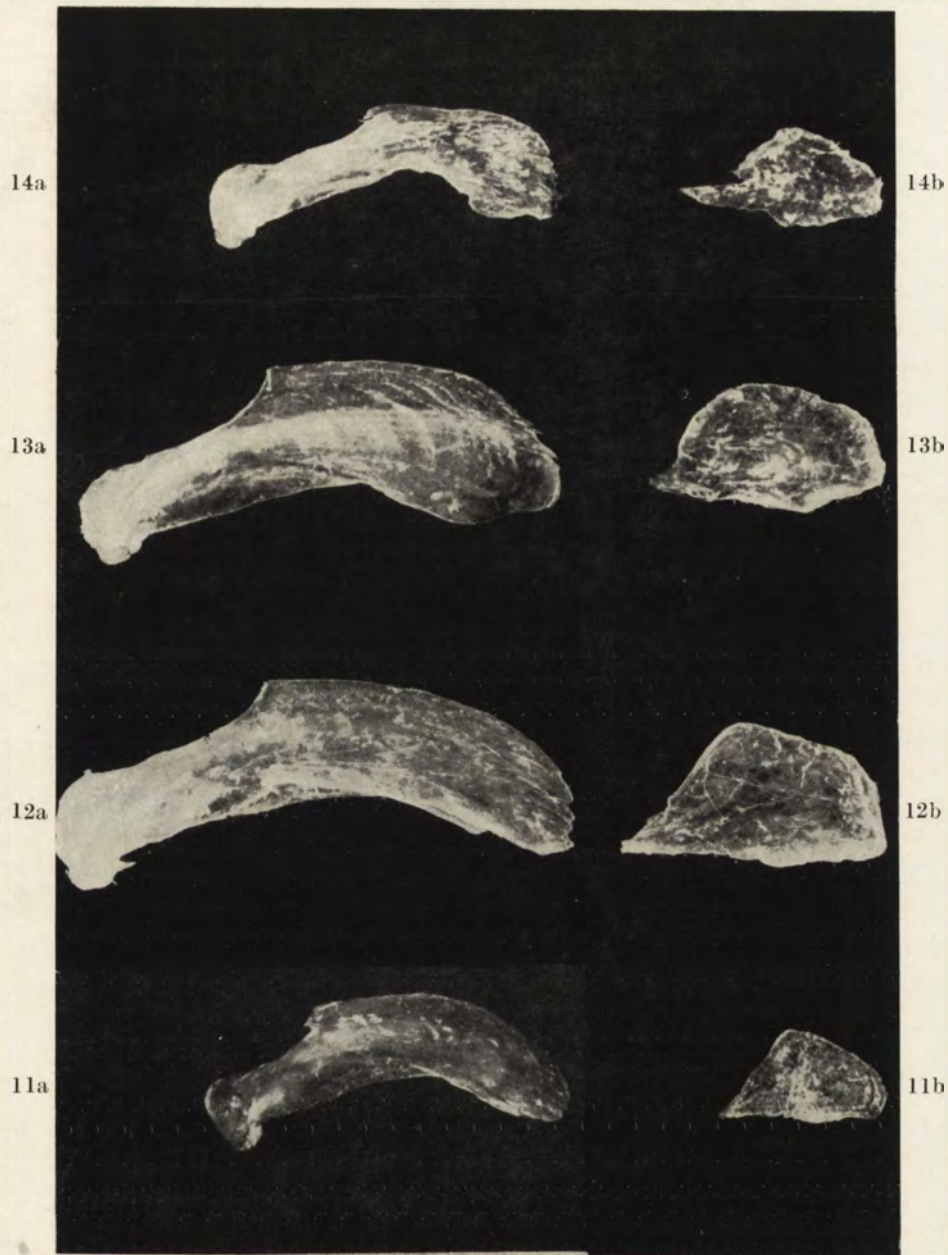
a — maxillare; b — supramaxillare of the *lavaretus*-group.
Coregonus lavaretus (L.)

Fig. 11. *Coregonus lavaretus polonica* KULMATYCKI, Puck Bay, Poland, 1924.

Fig. 12. *Coregonus lavaretus lavaretus* (L.), Puck Bay, Poland, 1958.

Fig. 13. *Coregonus lavaretus lavaretus* (L.) = „*C. nasus* (PALLAS)” sensu SVÄRDSON, Göta River, Sweden.

Fig. 14. *Coregonus lavaretus generosus* (L.), Tuczno Lake, Poland.



J. Stefaniak phot.

M. Gąsowska

Plate XXVI

a — maxillare; b — supramaxillare of the *lavaretus*-group.

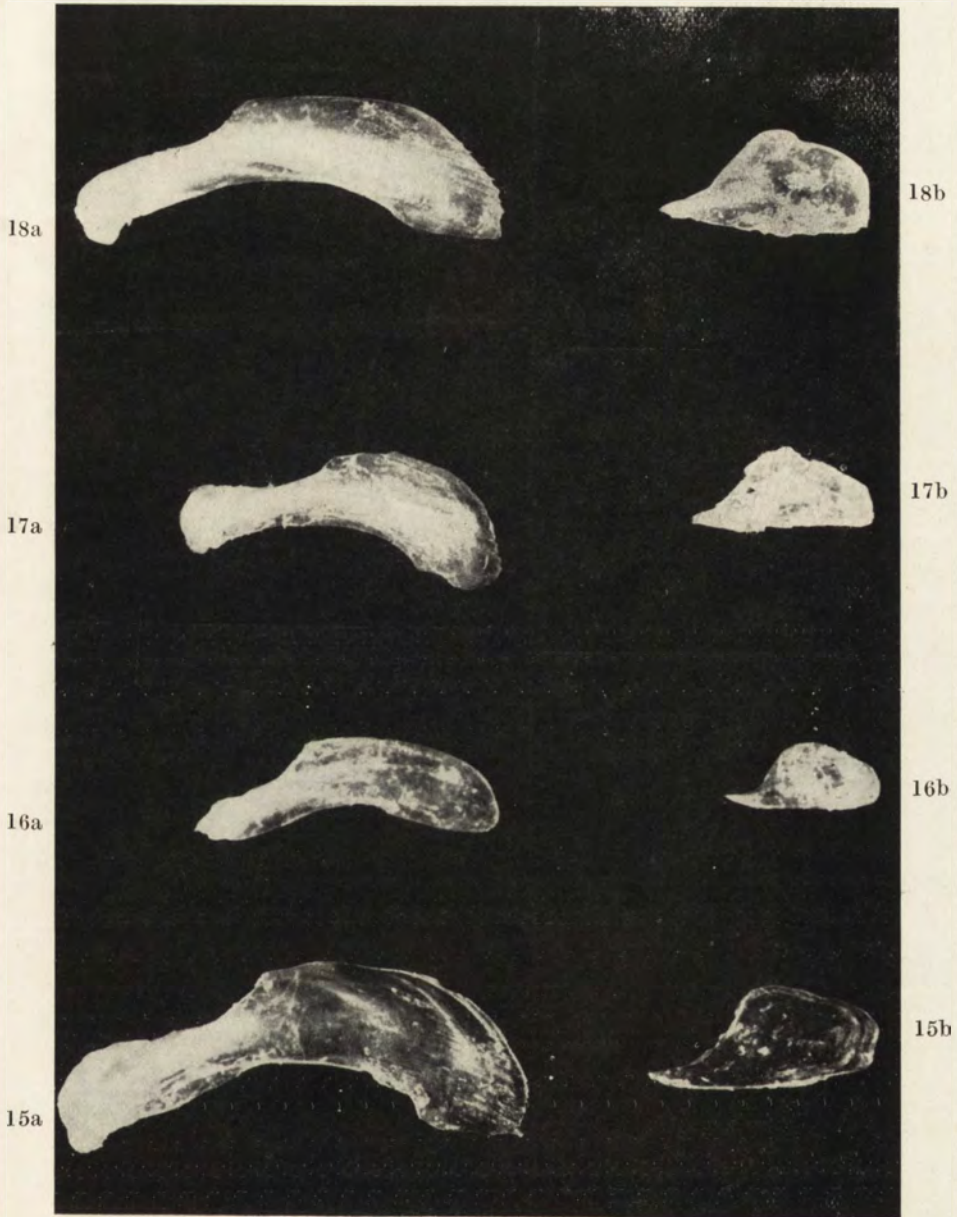
Coregonus lavaretus (L.)

Fig. 15. *Coregonus lavaretus maraena* (BLOCH), Miedwie Lake (Madüsko), Poland.

Fig. 16. *Coregonus lavaretus* infrasp. *oxyrynchus* (L.), Nord Sea.

Fig. 17. *Coregonus lavaretus acronius* RAPP, Boden Lake.

Fig. 18. *Coregonus lavaretus wartmanni* BLOCH, Boden Lake.



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Plate XXVII

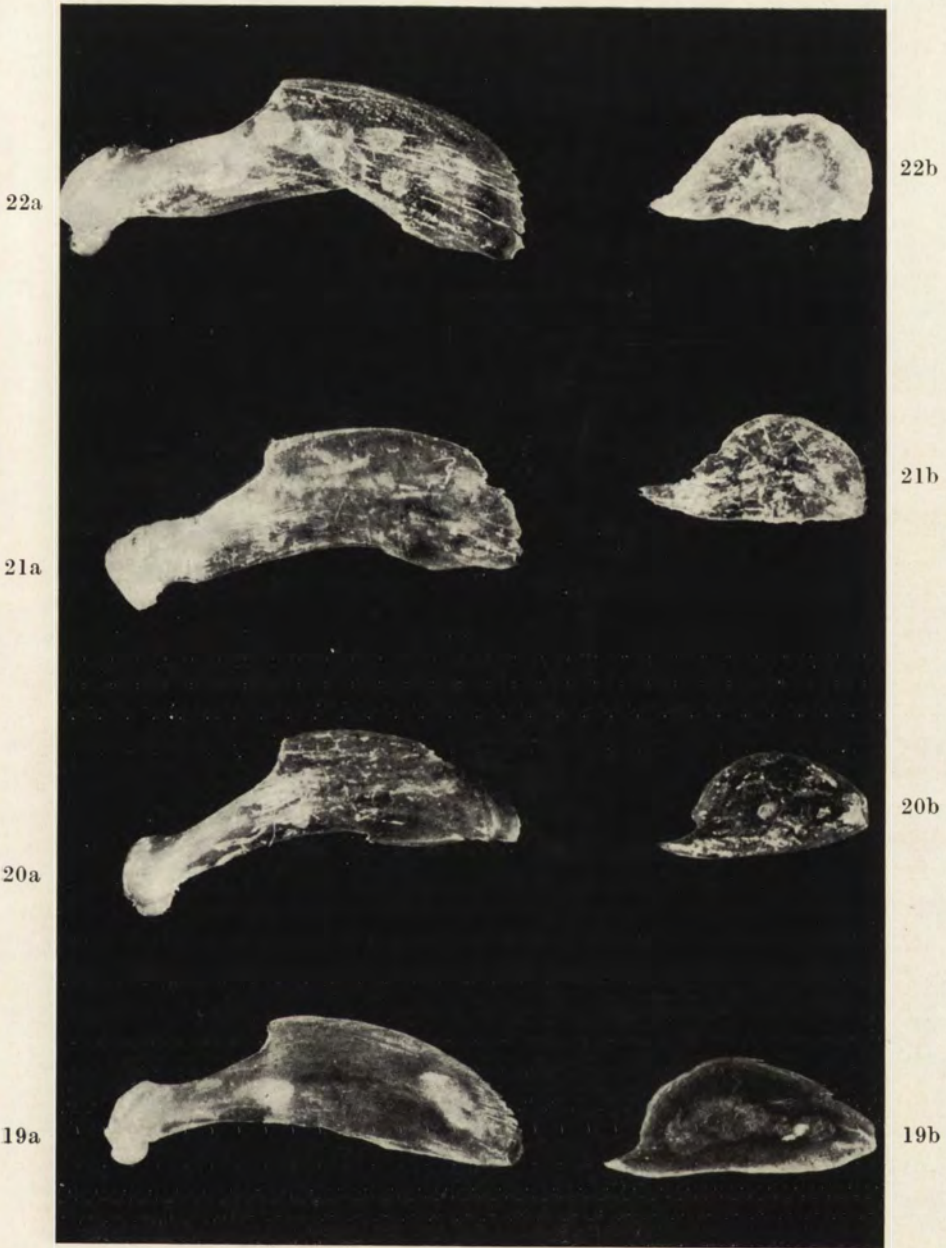
a — maxillare; b — supramaxillare of the *luvaretus*-group
Coregonus pidschian (GMELIN)

Fig. 19. *Coregonus pidschian* (GMELIN), Pechora River, USSR.

Fig. 20. *Coregonus pidschian chadary* DYBOWSKI, Amur.

Fig. 21. *Coregonus pidschian muksun* (PALLAS), mouth of the Lena River.

Fig. 22. *Coregonus pidschian clupeaformis* (MITCHILL), Canada.



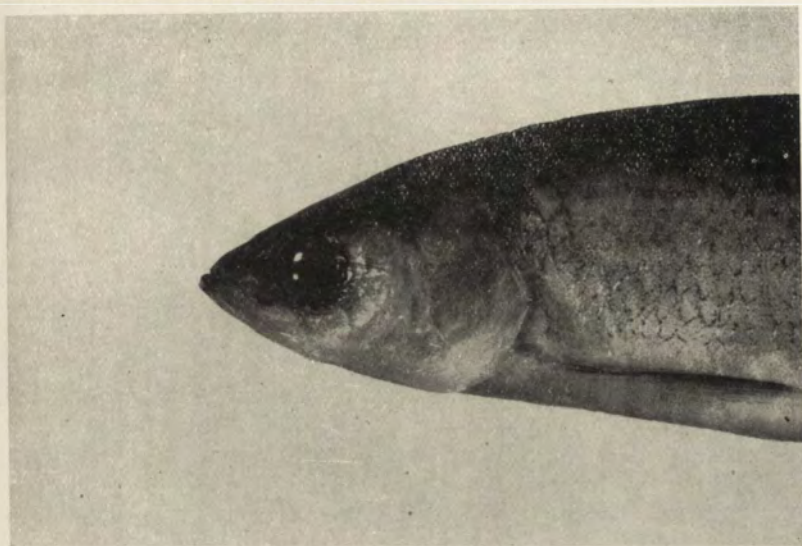
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Plate XXVIII

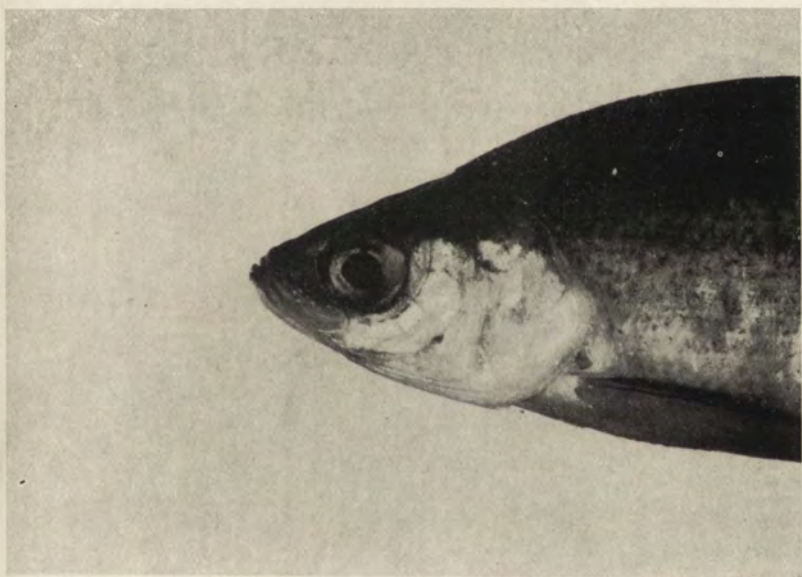
Fig. 23. *Coregonus albula* (L.), Wdzydze Lake, Poland.

Fig. 24. *Coregonus sardinella* VAL., Sibircha River, European Russia.

23



24

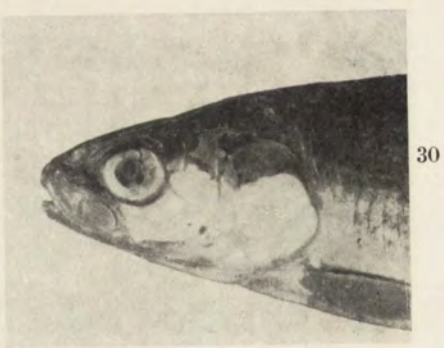
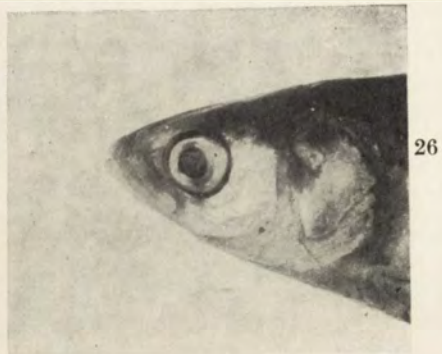


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Plate XXIX

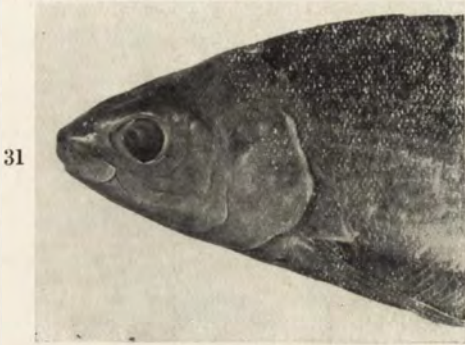
- Fig. 25. *Coregonus autumnalis* (PALLAS), Yugorski Shar Strait, USSR.
Fig. 26. *Coregonus artedi* (LE SUEUR), Lake Superior, America.
Fig. 27. *Coregonus tugun* (PALLAS).
Fig. 28. *Coregonus peled* (GMELIN), Andermei Lake, drainage of the Kara River.
Fig. 29. *Coregonus migratorius* (GEORGI), Baikal Lake.
Fig. 30. *Coregonus ussuriensis* BERG.



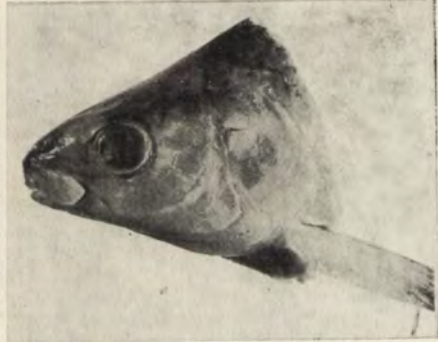
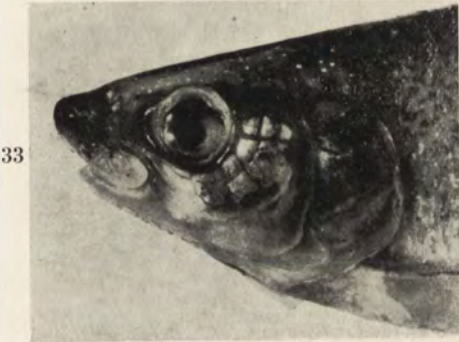
J. Stefaniak phot.
M. Gąsowska

Plate XXX

- Fig. 31. *Coregonus lavaretus polonica* KULMATYCKI, Puck Bay, Poland, 1924.
- Fig. 32. *Coregonus lavaretus lavaretus* (L.), Puck Bay, 1958.
- Fig. 33. *Coregonus lavaretus lavaretus* (L.) = „*C. nasus* (PALLAS)” sensu SVÄRDSON, Göla River, Sweden.
- Fig. 34. *Coregonus lavaretus generosus* PETERS, Tuczno Lake, Poland.



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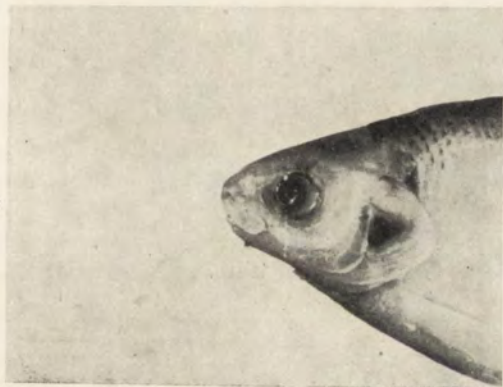
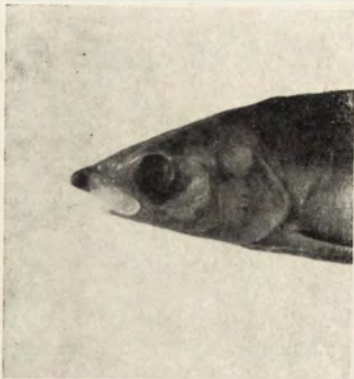
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J. Stefaniak phot.

M. Gąsowska

Plate XXXI

- Fig. 35. *Coregonus lavaretus maraena* (BLOCH), Miedwie Lake (Madüsee), Poland.
- Fig. 36. *Coregonus lavaretus* infraspp. *oxyrhynchus* (L.), Nord Sea.
- Fig. 37. *Coregonus lavaretus acronius* RAPP, Boden Lake.
- Fig. 38. *Coregonus lavaretus wartmanni* BLOCH, Boden Lake.

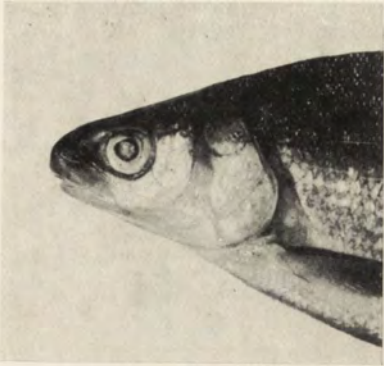


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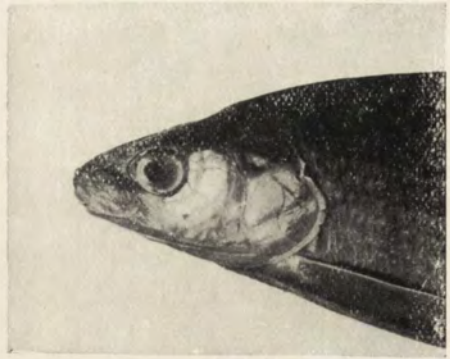
Plate XXXII

- Fig. 39. *Coregonus pidschian* (GMELIN), Pechora River, USSR.
Fig. 40. *Coregonus pidschian chadary* DYBOWSKI, Amur.
Fig. 41. *Coregonus pidschian muksun* (PALLAS), mouth of the Lena River.
Fig. 42. *Coregonus pidschian clupeaformis* (MITCHILL), coll. STAFF.
Fig. 43. *Coregonus pidschian clupeaformis* (MITCHILL), coll. VLADYKOV.

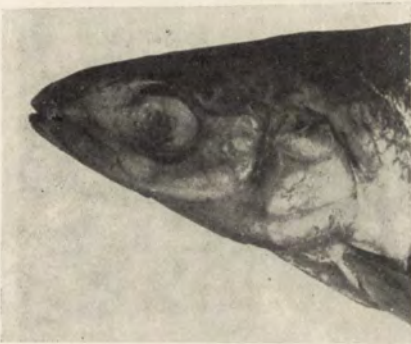
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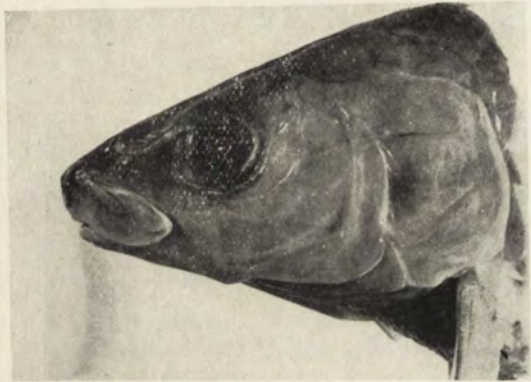
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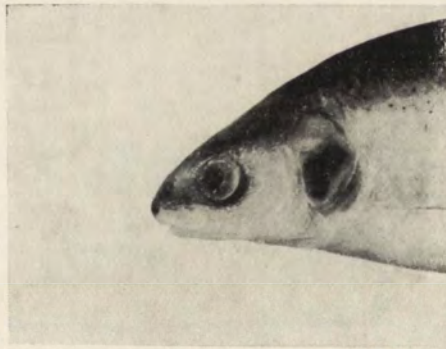
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