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Systematics

CRANIAL OSTEOLOGY OF THE WHITEFISH, *COREGONUS LAVARETUS* (L., 1758) FROM THE POMERANIAN BAY

OSTOLOGIA CZASZKI SIEI, *COREGONUS LAVARETUS* (L., 1758) ZATOKI POMORSKIEJ

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The Pomeranian Bay whitefish stock comprises two plastic forms: typical and humpback. Detailed morphological comparisons revealed significant differences between the two form with respect to certain characters. Cranial osteology of 60 individuals showed morphology of the dentary to be different in the two forms, the numerical expression of the differences showing their statistical significance. Values for the remaining characteristics analysed (a total of 21) were similar in the two forms. In addition, some cranial elements were found to be extremely variable. Measurement taken on few skulls only are, however, of a limited systematic value.

INTRODUCTION

Systematics of the genus *Coregonus* and the number of species the genus contains are not firmly established yet. Both Dorofejeva et al. (1980) and Rešetnikov (1980, 1988) list about 20 species. A lucid species classification is usually based on morphological criteria, including the anatomical ones. In the case of *Coregonus,* however, the characters are not so distinct. Frequently, the gill raker count was used as the most important diagnostic character, as e.g. in Svärdson (1957) who regarded the character to be genetically controlled. Later works (Gąsowska, 1960; Behnke, 1972) ceased to treat the gill raker count as a constant character, and so did Svärdson (1979) himself. In her preliminary revision of the genus *Coregonus*, Gąsowska (1960) attempted to prove a

considerable utility of shapes and proportions of the maxilla and supramaxilla. She
treated the gill raker count as a subordinate feature applicable in the intraspecific
systematics. In her systematics of the whitefish from the Soviet Union, Šapošnikova
(1968) additionally considered a number of plastic cranial characters.

The Pomeranian Bay is inhabited by ammigratory whitefish population spawning in
the Szczecin Lagoon. The population consists of two plastic forms: typical and
humpback (Fig, 1 and 2). The forms differ in certain plastic characters and, to some
degree, in the vertebral count (Heese, 1987).

Osteologic studies on the Pomeranian Bay whitefish skulls are aimed at comparing the
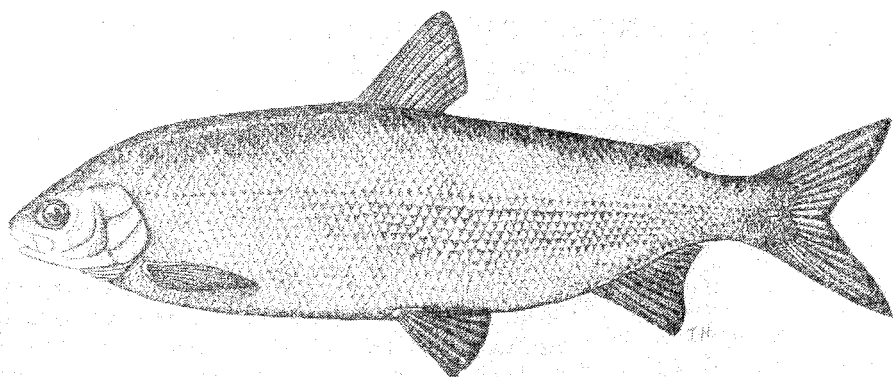two forms in terms of differences between the cranial bones and at determining the

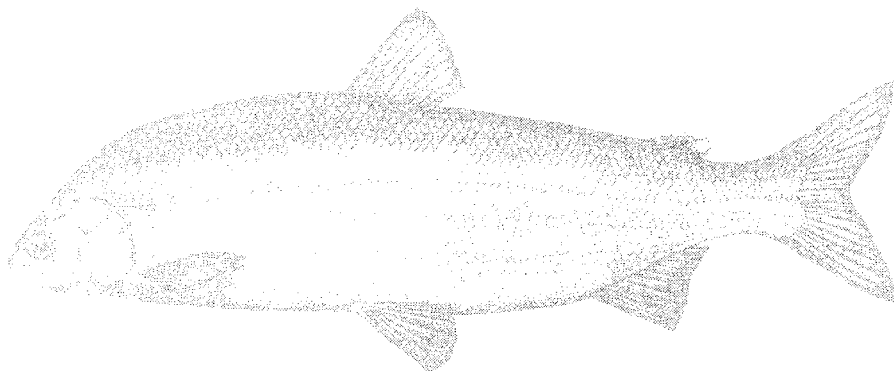Fig. 1. The Pomeranian Bay whitefish: typical form

Fig. 2. The Pomeranian Bay whitefish: humpback form

extent of variability of the characters analysed. The low number of osteological papers based on appropriate sample sizes makes comparison of the present results with the literature data very difficult.

MATERIALS AND METHODS

The whitefish to be studied were caught by commercial fisherman in November 1984 in the Pomeranian Bay off the mouth of the river Świna which forms a connection between the Szczecin Lagoon and the Bay. The Pomeranian Bay covers an inshore area between the coast and the 20-m depth contour and between Cape Arkona (Island of Rügen) and the Gąski lightohouse (Fig. 3).

A total of 60 whitefish individuals were examined, 30 belonging to the typical and 30 to the humpback form. Skull skin and muscles were removed by gradually treating them with hot water. Cranial measurements (Fig. 4) were taken as recommended by Šapošnikova (1968). Additionally, certain elements of the maxilla, supramaxilla, mesethmoid, posttemporal, and dentary were measured (Fig. 5). In the case of paired
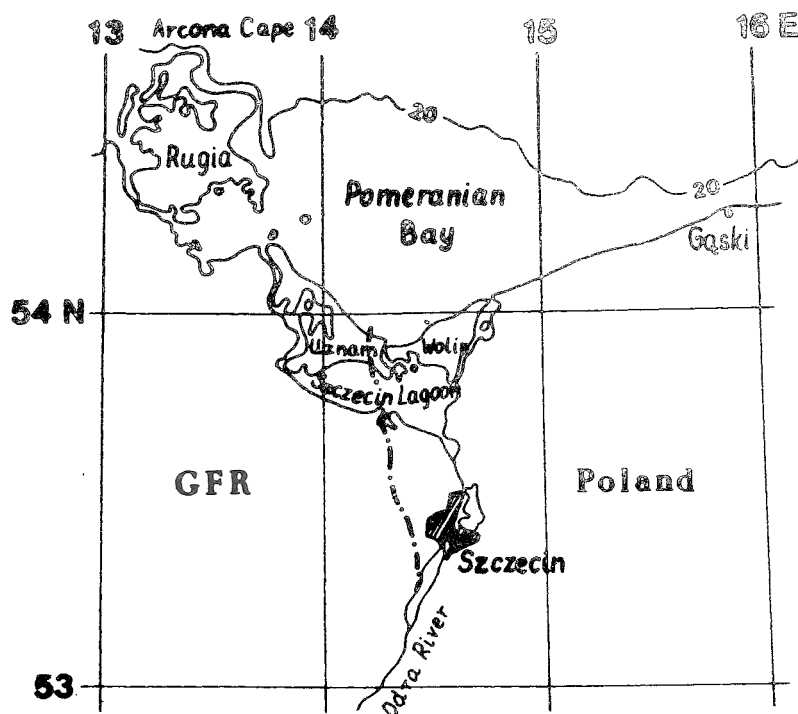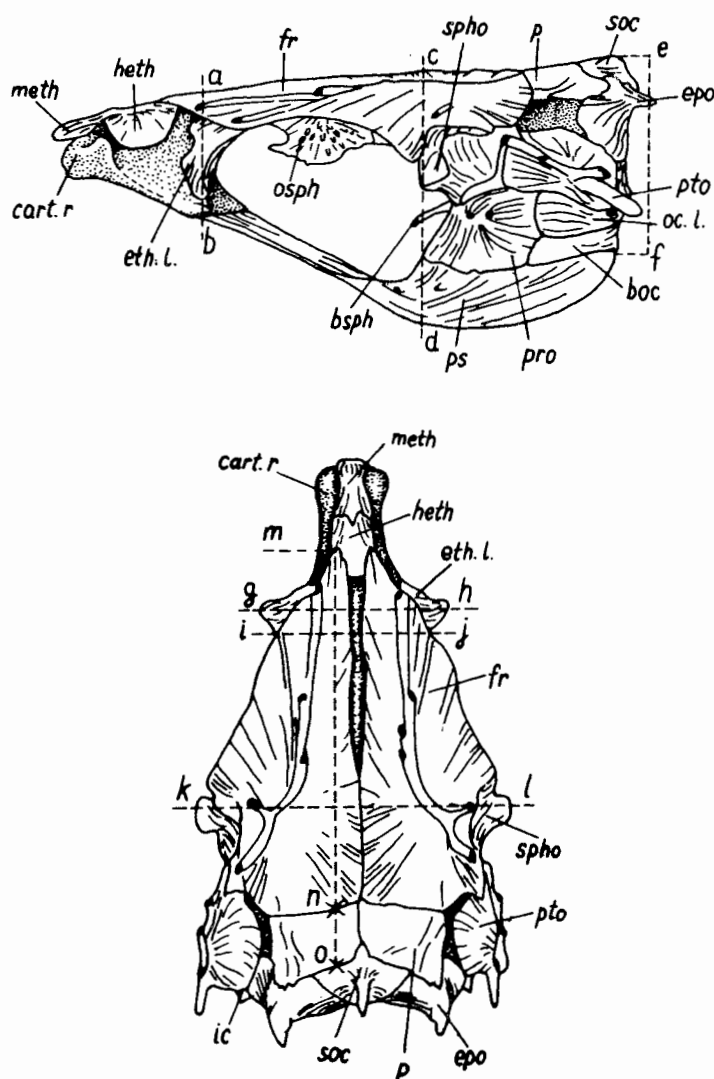

Fig. 3. Map of the Pomeranian Bay

Fig. 4. Diagram of cranial measurements.
ab = height at lateral ethmoid level; cd = height at prootic anterior margin level; ef= height from base
of basioccipital to end of supraoccipital; gh = width at lateral ethmoid level;
ij = width behind latera ethmoid; kl = width at sphenotic level;
mn = length of frontal; no = length of parietal. Cranial bones denoted as:
boc = basioccipital; bsph = basiphenoid; cart.r. = rostral cartilage; epo = epiotic;
eth.l. = lateral etmoid; fr = frontal; heth = hypethmoid; ic = intercalar;
meth = mesethmoid; oc.l. = lateral occipital; osph = orbitosphenoid; p = parietal;
pro = prootic; ps = parasphenoid; pto = pterotic; soc = supraoccipital; spho = sphenotic
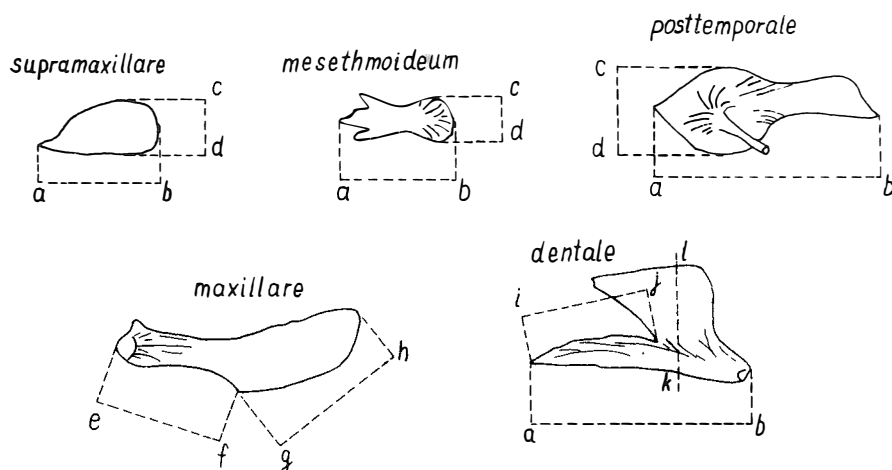
Fig. 5. Diagram of measurements on selected bones
ab = length; cd = width; ef = length of anterior part of maxilla; gh = length of
posterior part of maxilla; ij = distal length of dentary; kl = height of dentary

bones, those in the right side of the skull were measured. All the measurements were
made to 0.1 mm.

Statistical treatment of data involved calculations of mean values (M), standard errors
of the mean (m), standard deviations (S), and coefficients of variation (CV). The
differences were tested for significance by means of Student's t test. Confidence intervals
were calculated to facilitate statistical inference.

RESULTS

Tables 1 and 2 summarise morphological cranial characteristics of the typical and
humpback forms, respectively. Mean values for most characters are very similar in both
forms. The perceptible difference appear in an index representing the dentary height
expressed in per cent of the distal length of the bone. The index is 100.61% in the typical
form, which means that the mean height of the dentary is almost equal to its distal
length. On the other hand, the respectively humpback index is 96.2%. In other words, the
humpback dentary is more caved in (Fig. 6). Detailed data are given in Table 3. The
confidence interval for the difference at $\alpha = 0.05$ is as follows:

$$0.46 < m_1 - m_2 < 8.22$$

where: $m_1 = m$ of typical form
$m_2 = m$ of humpback form.

Table1

Cranial osteological characterisation of typical form of the whitefish

Character	n	Range	M±m	S	CV
Skull lemgth	30	45.4—66.5	54.09±0.95	5.20	9.6
skull length = 100					
Width at lateral ethmoid level	30	30.6—36.5	32.71±0.29	1.58	4.8
Width behind lateral etmoid	30	23.6—29.2	25.68±0.22	1.21	4.7
Width at sphenotic level	30	51.4—58.9	54.49±0.32	1.77	3.2
Height at lateral etmoid level	30	23.3—28.7	26.08±0.24	1.30	5.0
Height at prootic anterior margin level	30	41.3—46.6	43.39±0.26	1.45	3.3
Height from base of basiocc. to end of supraoccipital	30	38.0—44.6	40.03±0.31	1.68	4.2
Length of frontal	30	57.7—66.4	63.21±0.39	2.16	3.4
Length of parietal	30	5.4—12.6	9.16±0.31	1.75	19.1
Length of maxilla	30	40.4—50.5	44.5±0.45	2.49	5.6
Width of supram axilla	30	7.2—10.0	8.76±0.45	0.89	10.2
Length of supramaxilla	30	15.3—21.6	19.23±0.30	1.63	8.5
Width of mesethmoid	30	3.1—8.1	5.63±0.27	1.47	26.1
Length of mesethmoid	30	13.5—25.2	18.30±0.47	2.55	13.9
Width of posttemporal	30	14.0—19.5	16.38±0.27	1.46	8.9
Length of posttemporal	30	41.0—53.2	47.95±0.57	3.11	6.5
Length of dentary	29	34.9—44.3	40.94±0.40	2.11	5.2
Height of dentary	29	20.7—25.2	22.32±0.20	1.04	4.7
Length of posterior part of maxilla = 100					
Length of anterior part of maxilla	30	55.9—99.1	79.20±1.85	10.12	12.8
Length of supramaxilla = 100					
Width of supramaxilla	30	33.9—54.4	45.73±0.89	4.90	10.7
Length of posttemporal = 100					
Width of posttemporal	30	27.2—39.7	34.42±0.65	3.58	10.4
Length of dentary = 100					
Distal length of dentary	29	50.0—61.2	54.32±0.54	2.86	5.3
Height of dentary	29	51.4—61.3	54.61±0.55	2.91	5.3
Distal length of dentary = 100					
Height of dentary	29	86.7—119.0	100.61±1.37	7.23	7.2

Table 2

Cranial osteological characterisation of humpback form of the whitefish

| Character	n	Range	M ± m	S	CV
Skull length	30	45.6−66.7	56.11±1.02	5.59	10.0
Skull length = 100					
Width at lateral ethmoid level	30	29.5−37.1	32.22±0.29	1.61	5.0
Width behind lateral ethmoid	30	23.9−28.0	25.65±0.23	1.26	4.9
Width at sphenotic level	30	52.8−59.3	54.99±0.35	1.89	3.4
Height at lateral etmoid level	30	24.2−28.5	26.26±0.22	1.21	4.6
Height at prootic anterior margin level	30	40.8−47.2	43.78±0.26	1.45	3.3
Height from base of basiocc. to end of supraoccipital	30	38.0−41.4	39.76±0.22	1.22	3.1
Length of frontal	30	59.2−68.2	63.95±0.33	1.81	2.8
Length of parietal	30	5.5−12.1	8.64±0.30	1.63	18.9
Length of maxilla	30	40.8−49.4	44.85±0.34	1.84	4.1
Width of supramaxilla	30	7.4−11.1	8.71±0.16	0.89	10.2
Length of supramaxilla	30	17.1−21.3	18.83±0.20	1.11	5.9
Width of mesethmoid	30	3.3− 8.7	5.63±0.29	1.57	27.9
Length of mesethmoid	30	13.7−20.8	17.51±0.46	2.54	14.5
Width of posttemporal	30	14.3−19.7	16.63±0.27	1.46	8.8
Length of posttemporal	30	42.1−52.9	48.12±0.48	2.64	5.5
Length of dentary	30	37.9−46.1	41.85±0.34	1.86	4.4
Height of dentary	30	20.2−24.6	22.40±0.22	1.19	5.3
Length of posterior part of maxilla = 100					
Length of anterior part of maxilla	30	66.9−93.0	80.15±1.21	6.65	8.3
Length of supramaxilla = 100					
Width of supramaxilla	30	38.3−57.1	46.45±0.93	5.09	11.0
Length of posttemporal = 100					
Width of posttemporal	30	29.1−40.7	34.59±0.50	2.75	8.0
Length of dentary = 100					
Distal length of dentary	30	50.6−61.9	55.61±0.50	2.74	4.9
Heigth of dentary	30	46.9−58.7	53.42±0.57	3.13	5.9
Distal length of dentary = 100					
Heigth of dentary	30	86.0−116.8	96.27±1.35	7.40	7.7
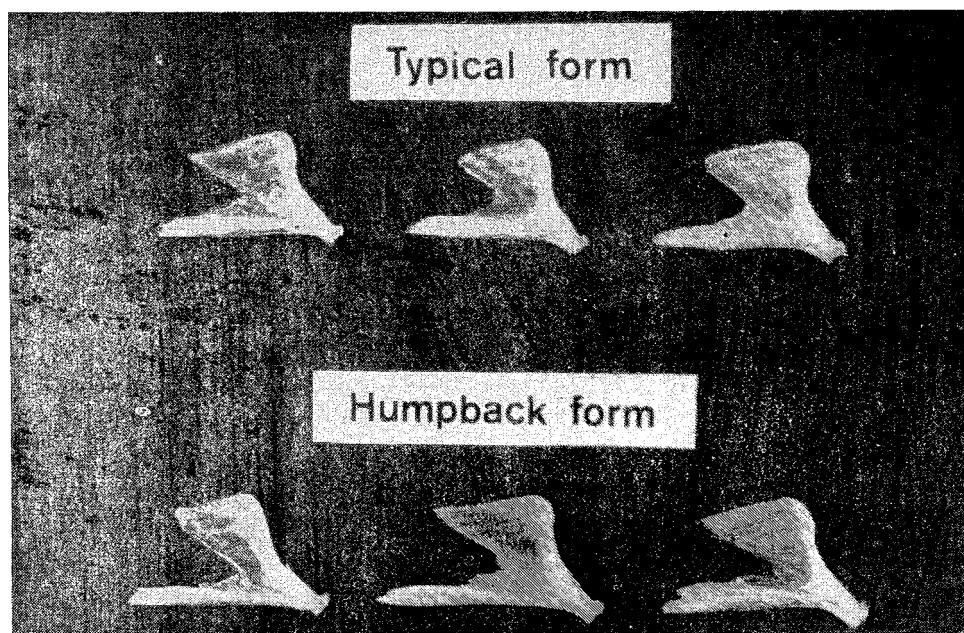
Fig. 6. Dentary in two plastic forms of the whitefish
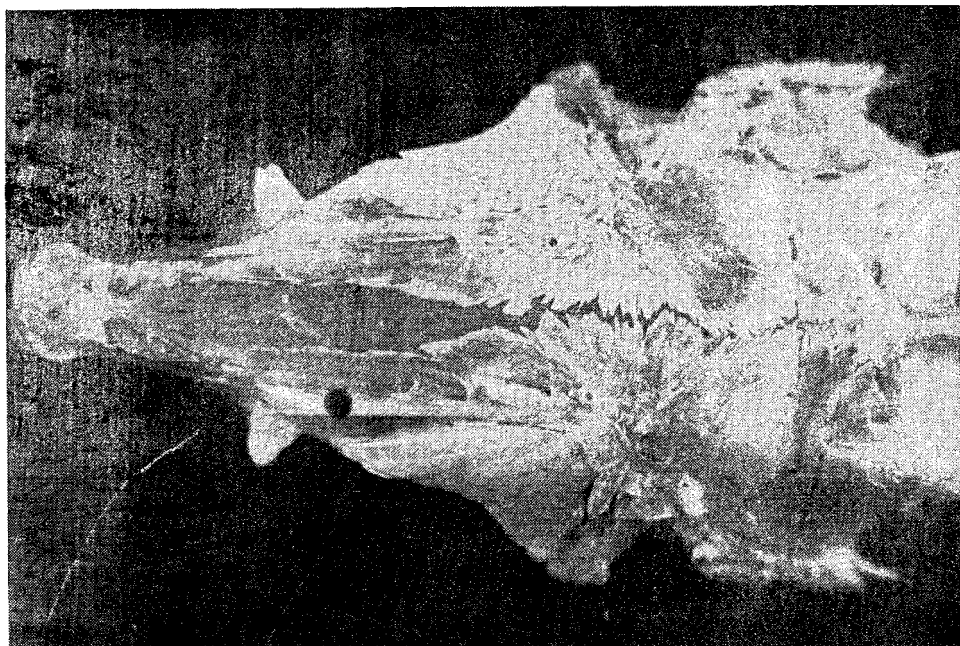

Fig. 7. Whitefish skull in dorsal view
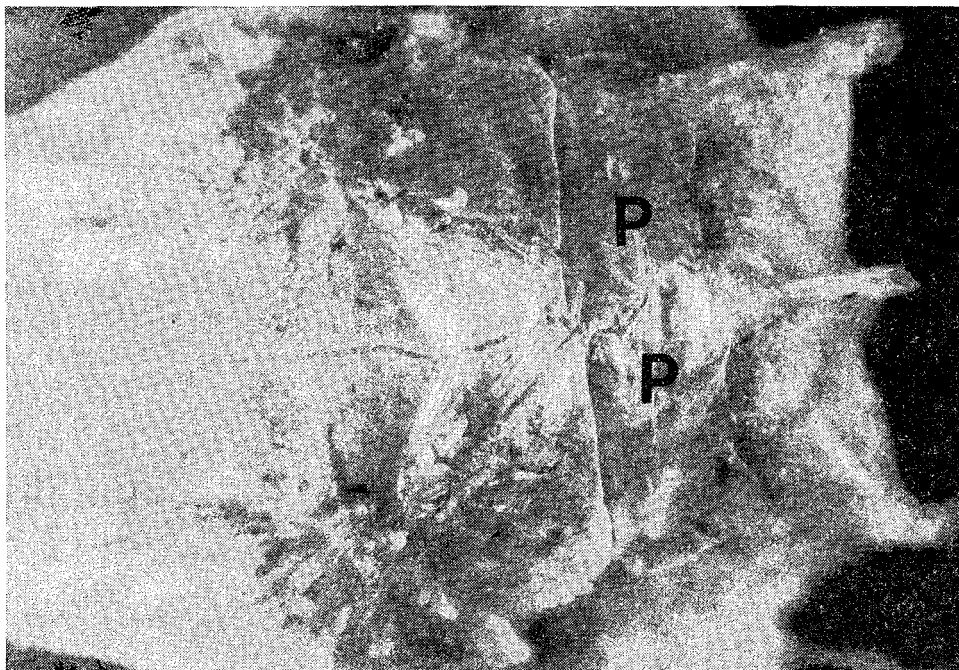
Fig. 8. Parietal bones (p) contacting along the entire length
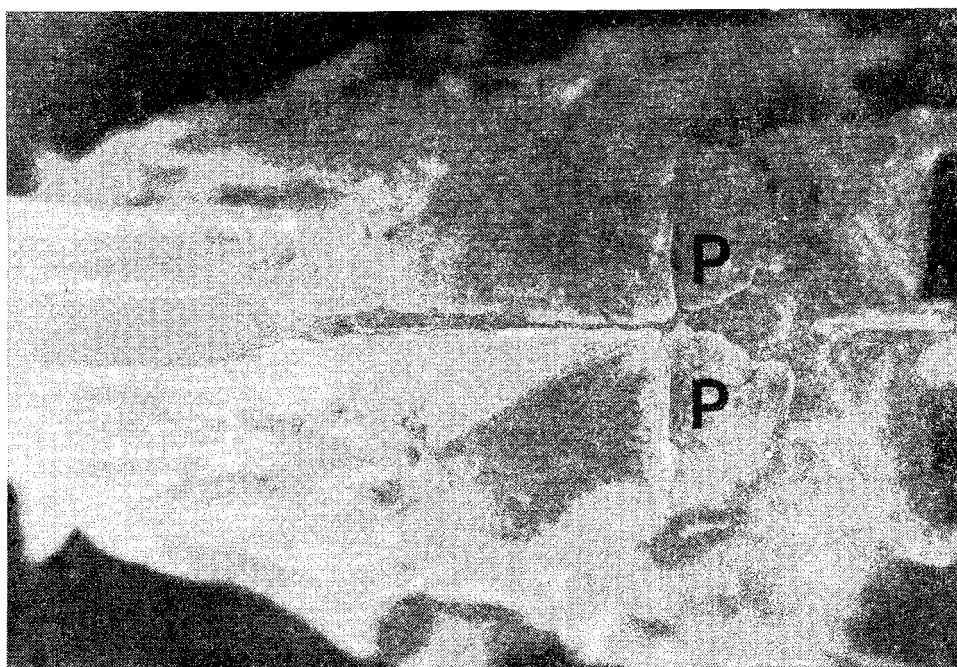

Fig. 9. Parietal bones (p) partially separated

<div align="right">Table 3</div>

Comparison of dentary proportions in typical and humpback forms,
significantly different at $\alpha = 0.05$

Character	Form	Range	M	F^{o}	$F_{0.05}$	t^{o}	$t_{0.05}$
		distal length of dentary = 100					
Height of dentary	typical	86.7−119.0	100.61	1.04	1.85	2.24	2.00
	humpback	86.0−116.8	96.27				

<div align="right">Table 4</div>

Arrangement of parietal bones in the whitefish forms studies

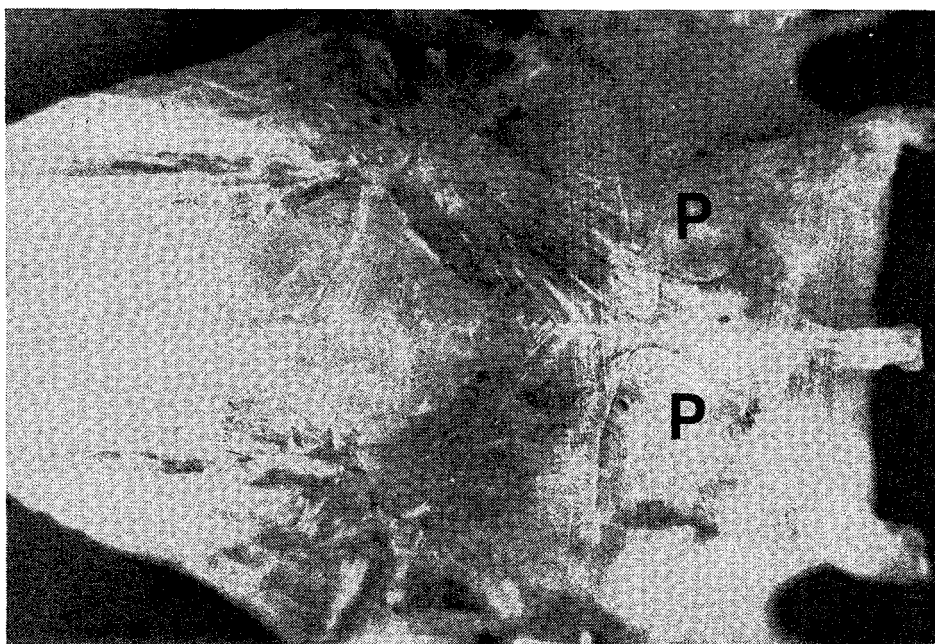| Sample size	Typical form			Humpback form		
	parietal arrangement			parietal arrangement		
	connected	connected partially	separated	connected	connected partially	separated
n	4	11	15	4	12	14
%	13.3	36.7	50.0	13.3	40.0	46.7

Fig. 10. Parietal bones (p) completely separated

Thus the mean value for the typical form exceeds the humpback mean by at least 0.46 and by 8.22% at the most.

Fig. 7 shows a whitefish skull in dorsal view. As seen from Tables 1 and 2, the most variable characters (CV ≥ 10%) include length of the parietal, width of the supramaxilla, length and width of the mesethmoid, and proportions in the maxilla, supramaxilla, and posttemporal. The parietal bone organization proved very variable and can serve as a basis for dividing the skulls examined into three groups. The first group contains skulls having the parietal bones contacting each other along their whole length (Fig. 8); in the second group, the bones are partially separated (Fig. 9), the separation being complete in the third (Fig. 10). Each whitefish form contained skulls belonging to all three groups (Table 4), the third group being the commonest arrangement.
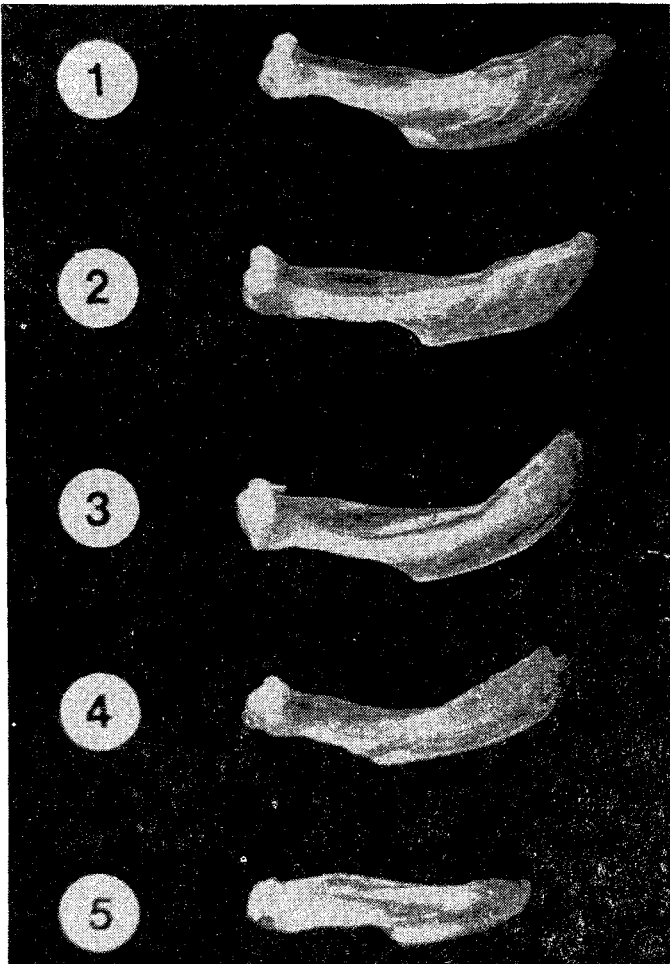

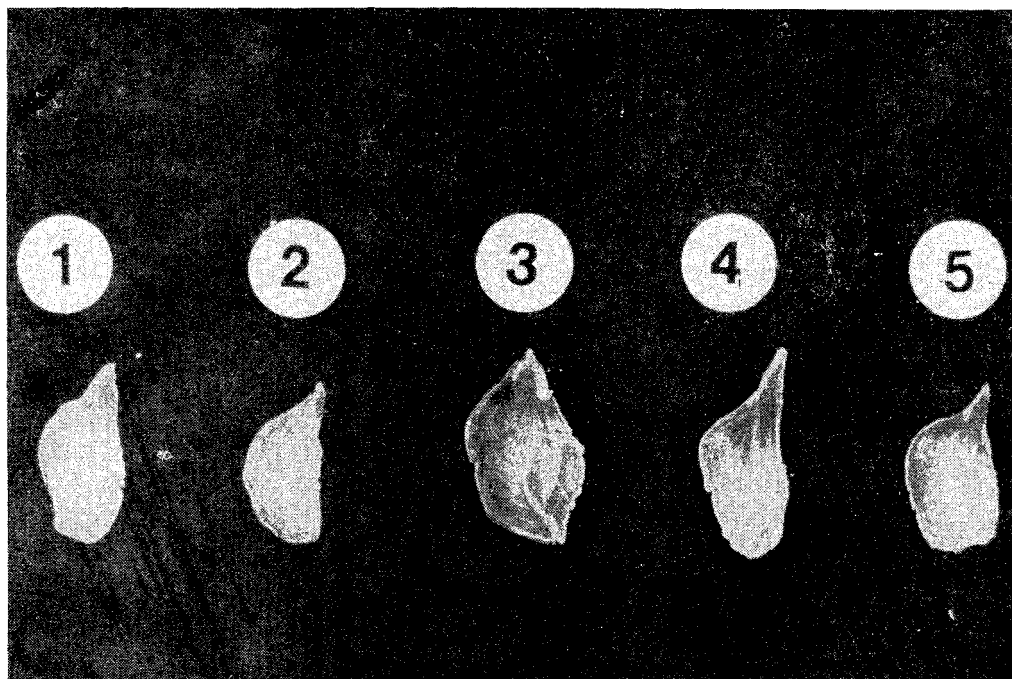Fig. 11. Different shapes of the maxilla
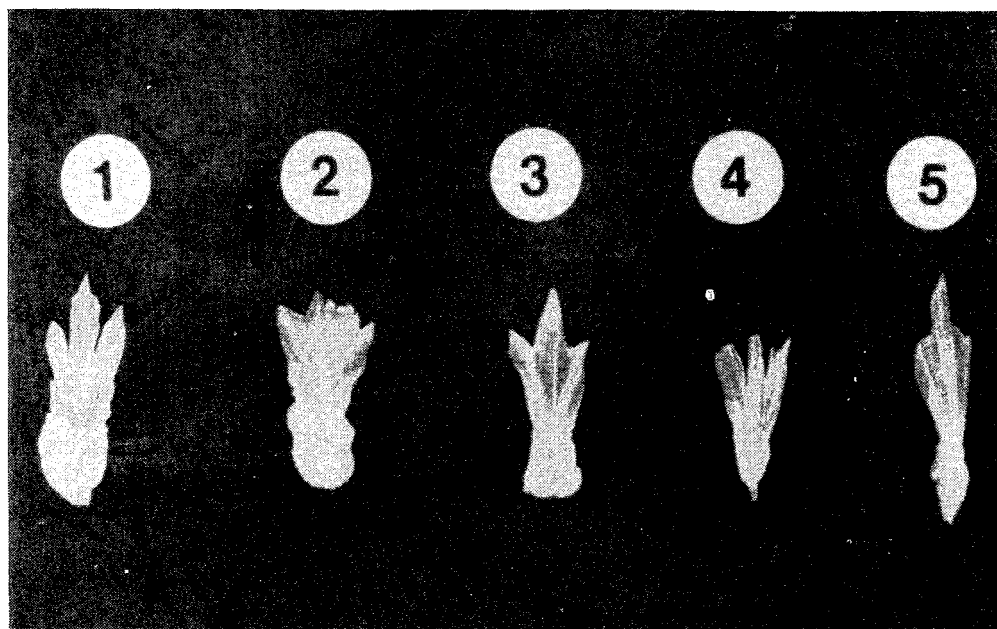
Fig. 12. Different shapes of the supramaxilla

Fig. 13. Different shapes of the mesethmoid

Shapes of the following bones: maxilla, supramaxilla, mesethmoid, and posttemporal are extremely variable and not always can be described by measurements or proportions. The maxillae presented in Fig. 11 are either arch-like curved or entirely straight. Their distal length is usually clearly longer than the proximal, but sometimes the two lengths are equal. Fig. 12 shows examples of the supramaxilla shapes ranging from strongly elongated and short to shortened in length and tall. The upper jaw of the whitefish additionally contains the premaxilla, in both forms covered with 5−8 fine teeth.

Exceptionally variable is the mesethmoid shape, the variability concerning width of the anterior plate and length of the shaft, the latter forked in a variety of ways (Fig. 13).
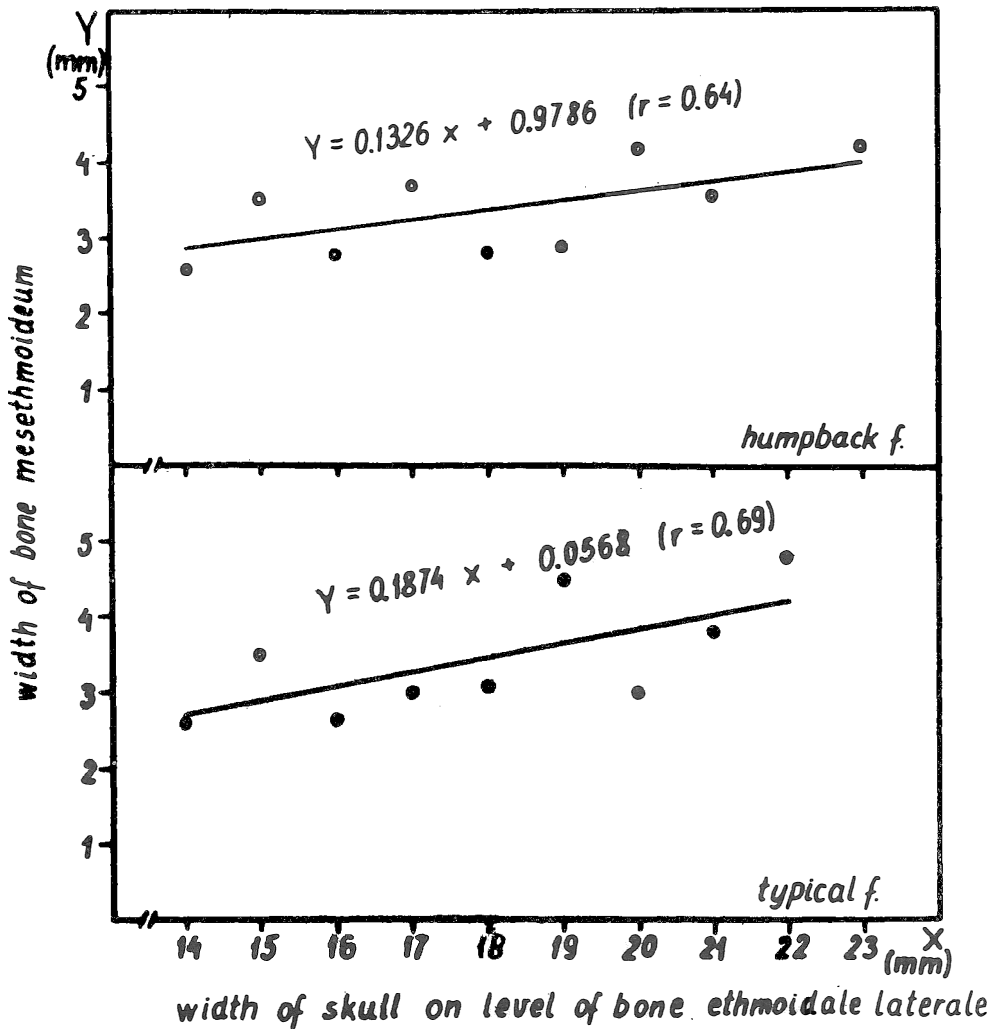

Fig. 14. Relationships between anterior plate of the mesethmoid and cranial width at the lateral ethmoid level

The anterior plate width depends on cranial width at the lateral ethmoid level (Fig. 14): the first increases with the other, the relationsjip holding for both forms but being more pronounced in the typical form.

The posttemporal is also very variable in shape, particularly in its lower part, strongly elongated and narrow or shovel-like flattened and short, connecting with the supracleithrum.

DISCUSSION

A comparison of the mean values calculated for the characters measured in the Pomeranian Bay whitefish with data reported by Šapošnikova (1968) for a number of subspecies reveals that the population under study is closest to *C. lavaretus ludoga* Poljakov and *C. lavaretus s. sp.* form the White Sea. Additionally, some characters are similar to those in *C. lavaretus pidschian* (Gmelin), *C. lavaretus pallasi* Pravdin, and *C. lavaretus maraenoides* Poljakov. It is only length of the frontal that differs the Pomeranian Bay whitefish from those studied by Šapošnikova (1968). In her cranial morphology-based identification key to the *C. lavaretus* subspecies, Šapošnikova described the mesethmoid anterior plate as very narrow in *C. lavaretus lavaretus* and wide in *C. lavaretus baicalensis*. Of the mesethmoids shown in Fig. 13, those with the widest anterior plates and short shafts resemble the description and drawing given by Šapošnikova for *C. lavaretus baicalensis*.

It should be emphasised that all cranial parameters of the Pomeranian Bay whitefish are totally different from those of *C. nasus* (Pallas) occurring in the Northern Ocean and Alaskan drainages. Therefore Svärdson's (1957) introduction of *C. nasus* (Pallas) sensu Svärdson to identify the sparse gill raker whitefish of the Baltic Sea and its drainage does not seem justified. On the other hand, Himberg (1970) put forward another view. He considered *C. nasus* (Pallas) sensu Svärdson and *C. pidschian* (Gmelin) to be conspecifics. A typical Northern Ocean's *C. pidschian* differs from the Baltic forms in. i.a. shape and proportions of the maxilla (Gąsowska, 1960; Šapošnikova, 1968). Gąsowska (1960) regarded this character as very important and used it to elevate *C. lavaretus pidschian* (a subspecies according to Berg, 1948) to the species level as *C. pidschian*. On the other hand, Rešetnikov (1980) failed to see firm justification for considering *C. pidschian* as a separate species. Biochemical assays and genetic studies (Lokšina, 1983; Kajdanova, 1983; and others) prove *C. nasus* to be the best defined coregonid species so far.

The high degree of polymorphism in meristic and plastic characters basically precludes adoption of any systematics proposed to date. The whitefish forms which developed identical phenotypes in European populations widely separated geographically can be regarded as members of a polytopic subspecies of the species *Coregonus lavaretus* (L.). As already known (Mayr, 1974a, b), such populations are not identical genetically. Because, however, a subspecies is not an evolutionary concept, such visually identical populations can be lumped into a joint taxon of a subspecies rank. An alternative, according to Mayr

(1974 a), is to give up separating the subspecies entirely. In view of a lack of diagnostic differences, any further subdivision of a polytopic subspecies into more subspecies differing only in their geographic location is hardly justified.

Based on the literature data, the already frequently quoted (Kaykorante and Mednikov, 1988) suggestion seems acceptable that the whitefish forms of the Baltic Sea drainage, Alps, and British Isles should be treated as *Coregonus lavaretus* (L., 1758) complex having a polytopic subspecies rank. The term "complex" is a neutral one and used informally (in terms of the Zoological Nomenclature Code); its usage becomes, however, indispensable in unexplained cases. I also suggest that the already existing names of species and subspecies be retained but preceded by the term "forma". The latter term ought to be used when it is difficult to judge whether a phenone at hand is a valid species, a subspecies, or a manifestation of individual variability. For example, to follow the concept expressed above, the name *Coregonus lavaretus generosus* (Peters) should be substituted by *Coregonus lavaretus forma generosus* (Peters). One of the Alpine whitefish, *Coregonus wartmanni* (Bloch) should be renamed *Coregonus lavaretus forma wartmanni* (Bloch). To retain the original names with inclusion of the "forma" seems purposeful for practical, zoogeographic and sometimes also historical reasons.

CONCLUSIONS

1. Osteologic examinations did not confirm the separate nature of the two plastic forms (typical and humpback) of the whitefish.
2. The basic dimensions of the skull as well as its width and length measured in different places show a relatively low variability.
3. Sahpes of maxilla, parietal, and mesethmoid are highly variable, which limits their taxonomic utility.
4. It seems necessary to collect data on cranial osteology of *C. lavaretus* from different geographic locations, based on representative sample sizes.
5. Both earlier works and the present study support the view that the whitefish of the Baltic Sea drainage, Alps, and British Isles should be treated as a polytopic subspecies *Coregonus lavaretus* (L., 1758) complex. In view of a lack of diagnostic differences, division of a single polytopic subspecies into more subspecies differing in their geographic location is not justified.

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ZATOKI POMORSKIEJ

STRESZCZENIE

Sieje do badań zostały złowione w listopadzie 1984 na Zatoce Pomorskiej w okolicach ujścia Świny. Na podstawie wcześniejszych badań morfologicznych pokroju ciała i cech merystycznych ustalono istnienie w tych wodach dwóch form plastycznych, typowej i wygrzbieconej.

Badania osteologiczne czaszki miały na celu porównanie jej budowy pomiędzy wróżnionymi formami i określenia zakresu zmienności analizowanych cech. Otrzymane średnie dla poszczególnych cech obu form są praktycznie bardzo do siebie zbliżone. Widoczne różnice pojawiają się dla indeksu przedstawiającego wysokość dentale wyrażną w % długości tylnej tej kości.

Badania osteologiczne nie potwierdziły jednoznacznie odrębności wyróżnionych form plastycz-
nych. Podstawowe wymiary czaszki jak jej szerokość i wysokość mierzona w różnych miejscach
charakteryzują się stosunkowo niską zmiennością. Wysoką zmienność kształtów obserwuje się dla
zespołu kości szczękowych, kości ciemieniowych i kości sitowej środkowej (*mesethmoideum*) przez
co przydatność ich dla celów taksonomicznych jest ograniczona.

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