

JACEK ŚWIDNICKI

OLIGOCENE ZEIFORMES (TELEOSTEI)  
FROM THE POLISH CARPATHIANS

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Osteology of the Zeiformes from the Menilite Beds (The Carpathian flysch) is discussed. The genus *Antigonia* (Caproidae) and *Zeus faber* are for the first time found to occur in the Carpathians. *Zenopsis* sp. from the Carpathians is a junior synonym of *Z. clarus* Daniltshenko from the Caucasus. Osteological characters of *Zeus hoernesii* show that it should be assigned to the genus *Zenopsis*. Osteological description of *Capros radobojanus* (Caproidae) from the Carpathians is given and a new species of *C. medianus* (Caproidae) is described. Comparison of osteological characters suggests that *Capros medianus* was not an ancestor of *Capros aper*; both species may have developed from a form close to *Capros radobojanus*.

**Key words:** Teleostei, taxonomy, Oligocene, Polish Carpathians.

Jacek Świdnicki, Instytut Zoologiczny, Uniwersytet Wrocławski, Sienkiewicza 21, 50-335 Wrocław, Poland. Received: March 1985.

## INTRODUCTION

This paper concerns the Zeiformes of the Oligocene Menilite Beds of the Carpathian flysch and gives their distribution in the profile of the Menilite Beds of the Units: Skole (sites: the hill Krępak near Korzeniec, Błazowa Rzeszowska), Subsilesian (Przysietnica) and Silesian (Rogi).

Numerous Zeiformes specimens were found during field work under supervision of Prof. A. Jerzmańska in the upper part of the profile of the Menilite Beds (1970—1984). The specimens, together with a collection examined earlier (Jerzmańska 1968), are the basis for this paper.

Geological descriptions of sites at the Krępak and at Błazowa Rzeszowska are given by Kotlarczyk (in press), those of the sites Rogi and Jamna Dolna by Jerzmańska (1968), Jerzmańska and Koltarczyk (1968). Detailed geological and paleontological description of the site Przysietnica is in preparation by Jerzmańska and Kotlarczyk.

Distribution of the studied zeids from the Oligocene Menilite Beds in the Polish Carpathians (ichthyofaunal zones according to Kotlarczyk and Jerzmańska 1976, 1977) is given in table 1.

Table 1

Distribution of the Zeiformes in the Menilite Beds in the Polish Carpathians

Assemblage	Ichthyofaunal zones	Zeiformes	Site
upper bathypelagic	IPM 6	<i>Capros medianus</i> sp.n. <i>Zeus faber</i>	Błażowa Rzesz. Błażowa Rzesz., Przysietnica
	IPM 5	<i>Zeus faber</i>	Krępak
	IPM 4	<i>Antigonia</i> sp. <i>Capros radobojanus</i> <i>Zeus faber</i>	Przysietnica
	IPM 3	no data	—
neritic sublittoral	IPM 2	<i>Capros radobojanus</i>	Rogi
lower bathypelagic	IPM 1	<i>Capros radobojanus</i> <i>Zenopsis clarus</i>	Jamna Dolna

The Recent Zeiformes include six families according to Greenwood *et al.* (1966), only Zeidae and Caproidae having fossil record. Both families have been known since Late Cretaceous (Gaudant 1977, 1978; Gayet 1980a, 1980b). The most controversial problem as regards families of the Zeiformes is relationship of the Caproidae. Some authors (Regan 1910; Berg 1955; Greenwood *et al.* 1966) considered that the Caproidae belonged to the Zeiformes, others (Günther 1860; Jordan 1923; Lindberg 1971) suggested a relationship with the Perciformes.

Gayet (1980a) assigned the Caproidae to the family Trachichthyidae of the order Beryciformes. Rosen (1984), basing on osteological analysis and on discussion of the Zeiformes relationship, forwarded a new hypothesis on the affinity of the Caproidae, which he regarded as a sister group of the remaining Zeiformes and Tetraodontiformes.

Recent comparative material: family Caproidae: *Capros aper* (6 specimens), *Antigonia* sp. (4 specimens); family Zeidae: *Zeus faber* (7 specimens), *Zenopsis conchifer* (3 specimens).

All the specimens described here are housed in the Paleozoological Department of the Zoological Institute, Wrocław University (abbreviated as ZPALWr.).

*Acknowledgments.*— My pleasant duty is to thank those whose kind help allowed me to make this contribution. I would like to thank very much Prof. A. Jerzmańska for her encouraging me to undertake a description of fossil Zeiformes from the Carpathians, for her help, her valuable advice and discussions. Thanks are due to Prof. J. Kotlarczyk for his help in looking for new localities in the Subsilesian Unit and for his advice on

geology. I would like to extend my thanks to Dr. A. F. Bannikov (Paleontological Institute, Moscow), who kindly lent me a specimen of *Zenopsis clarus* Danil., and to Dr. A. Kompowski (Fishery Oceanographic and Sea Renewal Institute, Szczecin), Dr. S. Krzykowski and T. Hesse M. Sc. (Ichthyological Institute of the Szczecin Agricultural Academy) and Dr. T. Linkowski (Sea Fishery Institute, Gdynia) for providing comparative material of the Recent Zeiformes. Thanks are due also to J. Błachuta M. Sc. from the Museum of Natural History, Wrocław University, for making specimens in his charge available to me, and to Dr. J. Jerzmański and E. Świdnicka M. Sc. for their help in field works. R. Adamski M. Sc. kindly made the photographs.

#### TERMINOLOGY AND ABBREVIATIONS

*Standard length* — from the anterior head end to the base of the middle rays in the caudal fin.

*Head length* — from the tip of snout to the end of operculum.

*Maximum body depth* — vertical distance from the dorsal body edge to the anterior end of anal fin base (genera *Zeus* and *Zenopsis*) or to pelvic fin base (genus *Capros*).

*Predorsal length* — from anterior end of upper jaw to first spine of dorsal fin.

*Preanal length* — from anterior end of lower jaw to anterior edge of anal fin base.

*Vertebrae counts* — vertebrae counted from the first, connected to the skull, to the last, formed by the first preural centrum and ural centra fused with it.

*Caudal vertebrae* — counted from the first vertebra, whose haemal spine is joined to the first interhaemal spine.

*Caudal peduncle* — section of body (or of backbone) from the vertical line at the end of the anal fin base to the middle ray base of the caudal fin.

<i>A</i>	— anal fin	<i>Ih</i>	— interhaemal spine, a pterygiophore supporting the anal fin ray
<i>Ang</i>	— angular	<i>Iop</i>	— interoperculum
<i>Art</i>	— articular	<i>In</i>	— interneural spine, a pterygiophore supporting the dorsal fin ray
<i>C</i>	— caudal fin	<i>Lac</i>	— lachrymal
<i>Chy</i>	— ceratohyal	<i>Mx</i>	— maxilla
<i>Cl</i>	— cleithrum	<i>Mpt</i>	— metapterygoid
<i>Cor</i>	— coracoid	<i>Nas</i>	— nasal
<i>Cos</i>	— rib	<i>Op</i>	— operculum
<i>Csoc</i>	— supraoccipital crest	<i>P</i>	— pectoral fin
<i>D</i>	— dorsal fin	<i>Pabd</i>	— postabdominal, bone septum bordering posteriorly abdominal cavity, formed by haemal spines of first caudal vertebrae and anterior interhaemal spines
<i>Den</i>	— dentary		
<i>Ecpt</i>	— ectopterygoid		
<i>Enpt</i>	— entopterygoid		
<i>Ep</i>	— epural		
<i>Etl</i>	— lateral ethmoid		
<i>Fr</i>	— frontal		
<i>Hyom</i>	— hyomandibular		
<i>Hhy</i>	— hypohyal		
<i>Hyp</i>	— hypural		

<i>Pal</i> — palatine	<i>Pop</i> — preoperculum
<i>Pap</i> — parapophysis	<i>Psd</i> — neural spine
<i>Par</i> — parietal	<i>Psv</i> — haemal spine
<i>Parh</i> — parhypural	<i>Qu</i> — quadrate
<i>Parp</i> — articular process of premaxilla	<i>Rbr</i> — branchiostegal rays
<i>Pas</i> — parasphenoid	<i>S</i> — scales
<i>Pasp</i> — ascending process of premaxilla	<i>Scl</i> — supracleithrum
<i>Pcl</i> — post-cleithrum	<i>Sop</i> — suboperculum
<i>Pelv</i> — pelvic bones; pelvic girdle	<i>Sy</i> — symplectic
<i>Pmx</i> — premaxilla	<i>V</i> — pelvic fin
PIN — Paleontological Institute, Academy of Sciences of the USSR	<i>Vert</i> — vertebrae
	<i>Vom</i> — vomer

## SYSTEMATIC PART

Superorder **Acanthopterygii** Greenwood *et al.*, 1966  
 Order **Zeiformes** (*sensu* Greenwood *et al.*, 1966)  
 Family **Zeidae** Bonaparte, 1831

The oldest representative of the family, *Palaeocyttus princeps* Gaudant, is known from the Cenomanian in Portugal (Gaudant 1978). The extinct genus *Palaeocentrotus* Kühne (1941) from the Paleocene in Denmark is considered now a representative of Lampridiformes (Bonde 1966). In his paper Bonde mentioned also a new genus of Zeidae in the Early Eocene. This form has not been described so far. Sorbini (1983) reports from the Middle Eocene in Monte Bolca a new genus and species, *Bajaichthys elegans* Sorbini. According to Daniltschenko (1960: 90), the data concerning the genus *Zeus* in the Georgian Eocene probably relate to the genus *Zenopsis*. In the Oligocene, an extinct form, *Cyttoides glaronensis* Wettstein, was known only from Glaris (Wettstein 1886). From among five Recent genera (Heemstra 1980) of this family the genus *Zenopsis* occurred in the Oligocene (Daniltschenko 1960, Jerzmańska 1968). Moreover, Horbatsch (1956) mentioned *Zeus* sp. from the Carpathians, and Kramberger (1891) described new species from the Late Oligocene in Styria: *Zeus robustus* and *Zeus hoernesii*. The latter species, cited from the Carpathians by Paucă (1938) and Jonet (1958) has been assigned to the genus *Zenopsis* (p. 122). *Zeus faber* is quoted from the Miocene of Oran (Arambourg 1927).

To exclude errors in identification of *Zeus* and *Zenopsis* their most important osteological characters have been compiled in table 2.

Genus *Zeus* Linné, 1758*Zeus faber* Linné

(pl. 50: 2a, b; figs. 1—4)

1927. *Zeus faber* Linné; Arambourg: 145, pl. 27: 4.1980. *Zeus faber* Linné; Heemstra: 8, pl. 2.

*Material.*—Seven incomplete imprints from: Błażowa Rzeszowska. (ZPALWr. A/2071), Krępak (ZPALWr. A/2066—2069), Przysietnica (ZPALWr. A/2063—2064; 2070).

Table 2

Diagnostic osteological characters of the genera *Zeus* Linné and *Zenopsis* Gill

No.	Character	<i>Zeus</i> Linné	<i>Zenopsis</i> Gill.
1	Horizontal line from the upper jaw joint to preoperculum lies	below lower orbit edge	on lower orbit edge
2	Mandibular quadrate articulation lies on a vertical	below anterior orbit edge	in front of anterior orbit edge
3	Upper end of the interoperculum	with notch	without notch
4	Number of caudal vertebrae	17 or 18	22
5	In caudal peduncle there are	two last vertebrae	three last vertebrae
6	Anal fin	IV/20-22	III/24—26
7	Squamation only in larger specimens <sup>1</sup>	cycloid scales small and thin	none
8	Bucklers along dorsal fin base	exclusively under soft rays	under spines and soft rays

<sup>1)</sup> According to Heemstra (1980) scales are not discernible on fish of the genus *Zeus* less than 12 cm in standard length.

Dimensions in mm:

	ZPALWr.	A/2068	A/2069
standard length		57.3	c. 79.0
head length		32.4	36.0
predorsal length		36.2	37.5
orbit diameter	c.	9.0	11.2
maximum body depth		28.7	c. 40.0

The standard length of these specimens is estimated from 3.5 cm to c. 20 cm.

**Description.** — **Skull.** In head structure characters 1, 2, 3 (table 2) were recognized. Other head bones (fig. 1) compared to Recent representatives of *Zeus faber* differ only in development of external edges of frontals. In two specimens (ZPALWr. A/2068—2069) the edges are clearly serrate in the section forming the upper orbit edge (fig. 1); this feature lacks in Recent *Z. faber* (in other known Miocene specimens described by Arambourg (1927) the anterior part of the frontals is unknown). The two have also traces of longitudinal ornamentation, as in Recent specimens.

**Vertebral column.** Thirty one short vertebrae (13+18). Parapophyses on 8th to 13th vertebrae (figs. 1, 2). Haemal spines on first two or three caudal vertebrae form the upper section of the postabdominal bone which borders the abdominal cavity posteriorly. The parapophysis of the last abdominal vertebra adheres to the haemal spine of the first caudal vertebrae (fig. 1). Neural spines are tilted in various directions and at various angles, similarly as they are in Recent specimens. The caudal peduncle structure is typical of *Zeus* (character 6, table 2).

**Pectoral fins.** Not wholly preserved. In the best preserved specimen there are 12 soft rays (fig. 2). The shoulder girdle as in Recent *Z. faber* (fig. 1).

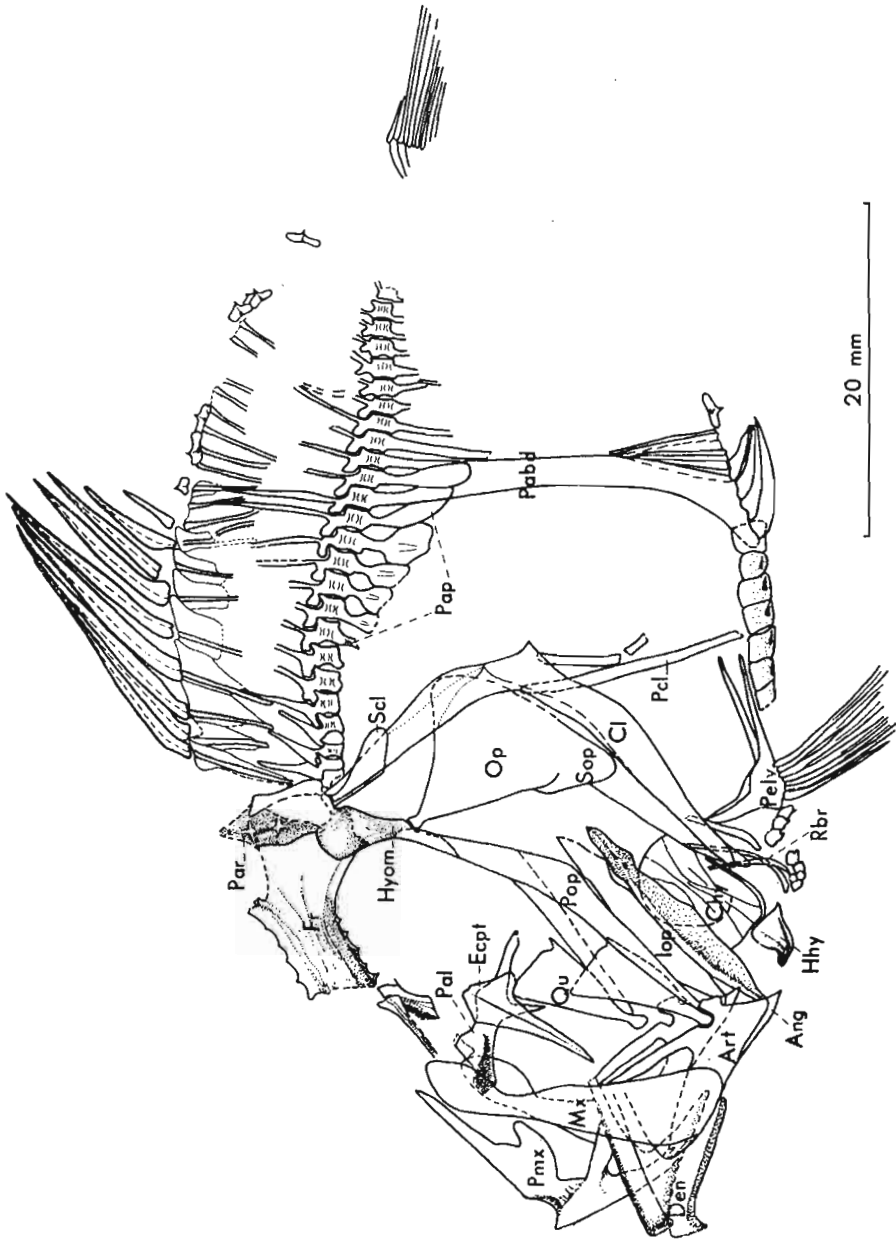


Fig. 1. *Zeus faber* Linné, ZPALWr. A/2068, menilite shales, zone IPM 5, Krępak.

**Pelvic fins.** It is difficult to establish the number of rays as imprints of both fins overlap. There were probably 7 rays, 1 being somewhat wider at the base, unbranched, and 6 being branched. Along the ventral edge of the body behind and in front of pelvic fins there are bucklers armed with one spine. Seven bucklers lie in one line between the anal fin and the pelvic fins, and eight bucklers are loosely situated in front of pelvic fins.

**Dorsal fin.** The spinous fin consists of 9 or 10 spines, the third being the longest. The soft fin has not been preserved completely in any specimen. The number of interneural spines shows that there are about 21 soft rays (fig. 2). Along the base

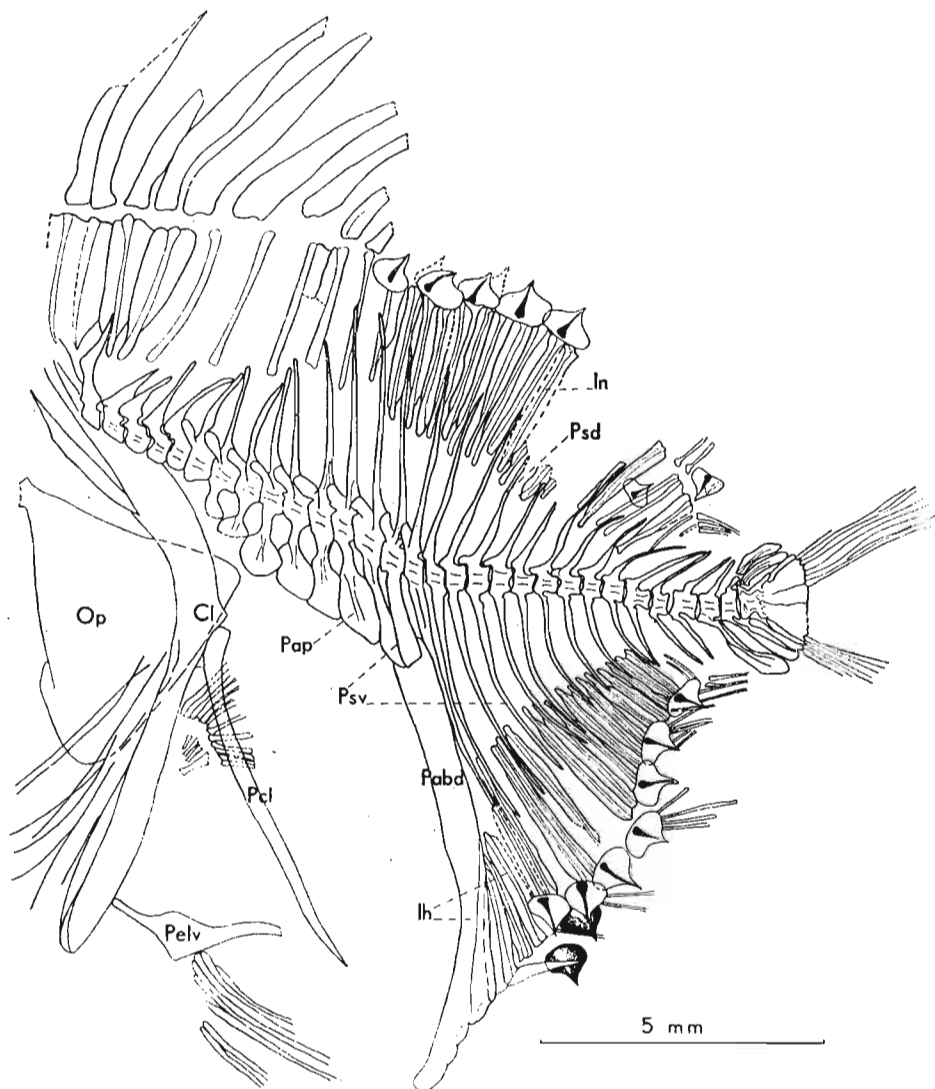


Fig. 2. *Zeus faber* Linné, ZPALWr. A/2071, menilite shales, zone IPM 6, Błazowa Rzeszowska.

of the soft dorsal fin there are bony bucklers (character 8, table 2) with two spines. In the best preserved specimen (ZPALWr. A/2071) there are only 5 anterior bucklers in one row and two loosely arranged (fig. 2). Bucklers on the posterior part of this fin are not preserved. The bucklers differ somewhat in shape. In some specimens their bases are low and elongate, the main spine being posterad. In others the bases are short, the main spine being roughly perpendicular to the dorsal edge of the body (figs. 1, 2, 4).

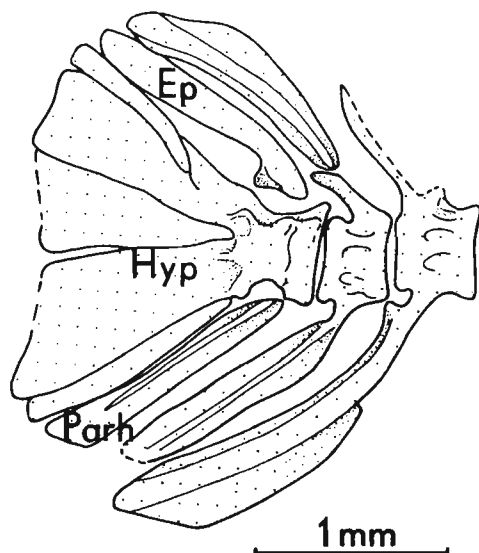


Fig. 3. *Zeus faber* Linné, ZPALWr. A/2071, caudal fin skeleton, menilite shales, zone IPM 6, Błażowa Rzeszowska.

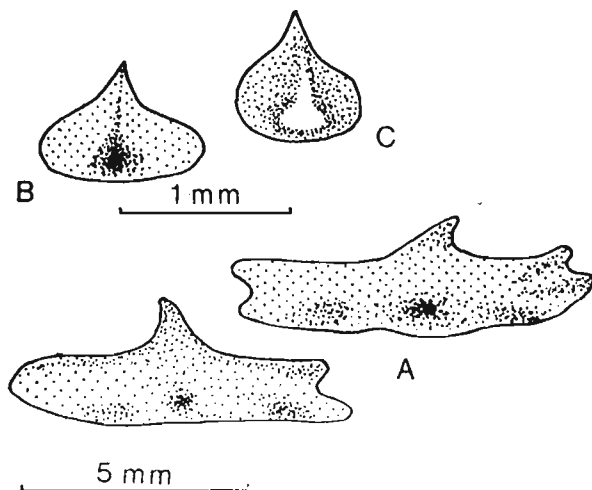


Fig. 4. *Zeus faber* Linné, A ZPALWr. A/2067, bone bucklers, external surface imprint, menilite shales, zone IPM 5, Kępak; B ZPALWr. A/2071, bone buckler, external surface imprint, menilite shales, zone IPM 6, Błażowa Rzeszowska; C ZPALWr. A/2071, bone buckler, external surface, menilite shales, zone IPM 6, Błażowa Rzeszowska.



**Anal fin.** Of four spines (character 6, table 2) three anterior ones are situated on the first pterygiophore (fig. 1), the last spine is on the next one. The soft fin incompletely preserved. Judging from the number of pterygiophores, 20 soft rays probably occur. In a well-preserved imprint of the anal fin there are traces of 7 bucklers in one row along the base of the fin. The bucklers have two spines each, and do not differ in shape from those along the soft dorsal ray.

**Caudal fin.** Thirteen rays and two accessory ones. Poor preservation of the ray ends does not allow to reconstruct the fin shape. Skeletal structure of the caudal fin typical of *Zeus faber* (figs. 2, 3).

Very well preserved cycloidal scales (character 7, table 2) were found only in the largest specimen (ZPALWr. A/2066, pl. 50: 2a, b).

**Remarks.**—As all osteological characters were found to be typical of the genus *Zeus* (table 2), the forms under study were compared with Recent representatives of *Z. capensis* and *Z. faber*, and with Miocene specimens of the latter (Arambourg 1927). Both species differ in the structure and number of bucklers along the soft dorsal and anal fin base, which can be observed in fossils, as well. In *Z. capensis* the bucklers have only 1 spine, in *Z. faber* — 2 spines (Cuvier and Valenciennes 1835; Günther 1860; Arambourg 1927; Heemstra 1980), just as in the studied specimens. The number of bucklers at the base of soft dorsal and anal fins is within the variability range of Recent *Z. faber* (Heemstra 1980: 10, tab. 1).

On the basis of the obtained data the studied forms should be considered the earliest representatives of *Zeus faber*.

Analysis of descriptions and illustrations of Oligocene *Z. robustus* and *Z. hoernesii* (Kramberger 1891: pl. 1: 1—8, pl. 4: 1—3) shows that only the former may be assigned to the genus *Zeus*, because it displays short caudal section in backbone, cycloidal scales and short caudal peduncle (characters 4, 7, 5 in table 2); *Z. robustus* needs a revision. The characters of *Zeus hoernesii* (p. 122) are diagnostic of the genus *Zenopsis*.

**Stratigraphic and geographic distribution.**—Recent: eastern Atlantic (from Norway to Southern Africa), the Mediterranean, Black Sea, Australia, New Zealand, Japan, Korea, eastern shores of Southern Africa to the Delagos Bay.

Miocene: Northern Africa (Oran). Oligocene: Polish Carpathians (Błażowa Rzeszowska, Krępak, Przysietnica).

Genus *Zenopsis* Gill, 1863  
*Zenopsis clarus* Daniltshenko, 1960  
(fig. 5)

1960. *Zenopsis clarus*; Daniltshenko: 88, pl. 10: 1; fig. 18.

1968. *Zenopsis* sp.; Jerzmańska: 441; pl. 5: 2.

**Material.**—Two complete imprints of juvenile specimens from the site Jamna Dolna (ZPALWr. A/860 and 2062).

Dimensions in mm of juvenile specimen (ZPALWr. A/2062):

standard length	14.0
maximum body depth	10.3
head length	2.1
pre-dorsal distance	7.9
dorsal fin base length	8.6
pre-anal distance	12.1
anal fin base length	6.8

*Description.*—**Skull.** Structure typical of the genus *Zenopsis* (characters 1, 2 in table 2).

**Vertebral column.** Thirty five vertebrae (13+22), including the first abdominal vertebra, the neural arch of which fuses with the skull. The centra of first four vertebrae are eclipsed by cleithrum and supracleithrum; beginning with the fifth abdominal vertebra are both centra and neural arches well visible. Parapophyses on 9th to 13th vertebrae (fig. 5). Haemal spines of first four caudal vertebrae form the upper part of the postabdominal (fig. 5). The structure of caudal peduncle typical of *Zenopsis* (character 5, table 2).

**Pectoral fins.** Rays are not preserved. Supracleithrum well visible. Cleithrum reaches the ventral body edge in front of pelvic fin base. Post-cleithrum, bayonet-shaped, in contact with the ventral edge behind pelvic fins. Coracoid poorly visible (fig. 5).

**Pelvic fins.** There are six branched rays and one unbranched. The pelvic girdle contacts the cleithrum and coracoid by its anterior end, and by posterior processes it contacts the post-cleithrum (fig. 5).

**Dorsal fin.** Nine strong spines and 24 soft rays, judging by 24 pterygiophores. Along the base of this fin (character 8, table 2) there are traces of 14 bony bucklers, nine along the soft, five along the spinous fin (fig. 5). On each buckler one spine, perpendicular to dorsal body edge (fig. 5).

**Anal fin.** Three strong spines (character 6, table 2), the first being the longest, the third the shortest. Two anterior spines on the first pterygiophore. The lower section of the postabdominal is formed by two anterior pterygiophores. The presence of 23 pterygiophores shows there were 23 soft rays. Ten bucklers are parallel to the base of this fin, each with one spine.

The caudal fin skeleton is poorly preserved. 13 rays, and two accessory ones.

Seven paired bucklers along the lower body edge, between the anal fin and the base of pelvic fins; in the specimen from Caucasus (PIN 1413/635) there are even eight. Between the head and the pelvic fins in the Caucasian specimens there are 7—8 bucklers, forming a tight row (Prof. A. Jerzmańska's personal communication). In the studied material in one specimen (ZPALWr. A/860) only six last bucklers of this row were found. The state of preservation of the bucklers of this section of the specimen ZPALWr. A/2062 suggests, however, that at least two bucklers near pelvic fins (fig. 5) might have been paired, in contrast to others, unpaired. This seems to be supported also by traces of bucklers in the *Zenopsis clarus* imprint from the Caucasus (PIN 1413/635). Moreover, on the bilateral imprint from the Carpathians (ZPALWr. A/860) the spines on several bucklers in this line are marked by depressions. This may evidence that on the left and the right side of the specimen there were two opposite rows of bucklers.

The above observations allow to infer that in *Z. clarus* there were at least two paired bucklers in front of the pelvic fins apart from several unpaired anterior bucklers. In Recent *Z. conchifer* there are only 2 or 3 unpaired bucklers in this part of the ventral edge.

*Remarks.*—On the basis of the description by Daniltshenko (1960), and analysis of the structure of the specimen PIN 1413/635 as well as Prof. Jerzmańska's personal communication, no essential differences were found between Carpathian specimens and *Zenopsis clarus* from the Caucasus. The difference in the number of bucklers along the soft dorsal and anal fins in specimen from the Carpathians may result from individual variability in *Z. clarus*.

As regards the overall number of bucklers along the dorsal fin *Z. clarus* is close to the Recent *Z. nebulosus*, while differing clearly from *Z. conchifer*. The two Recent species have, according to Heemstra (1980), 12—15 and 7 bucklers respectively along the dorsal fin.

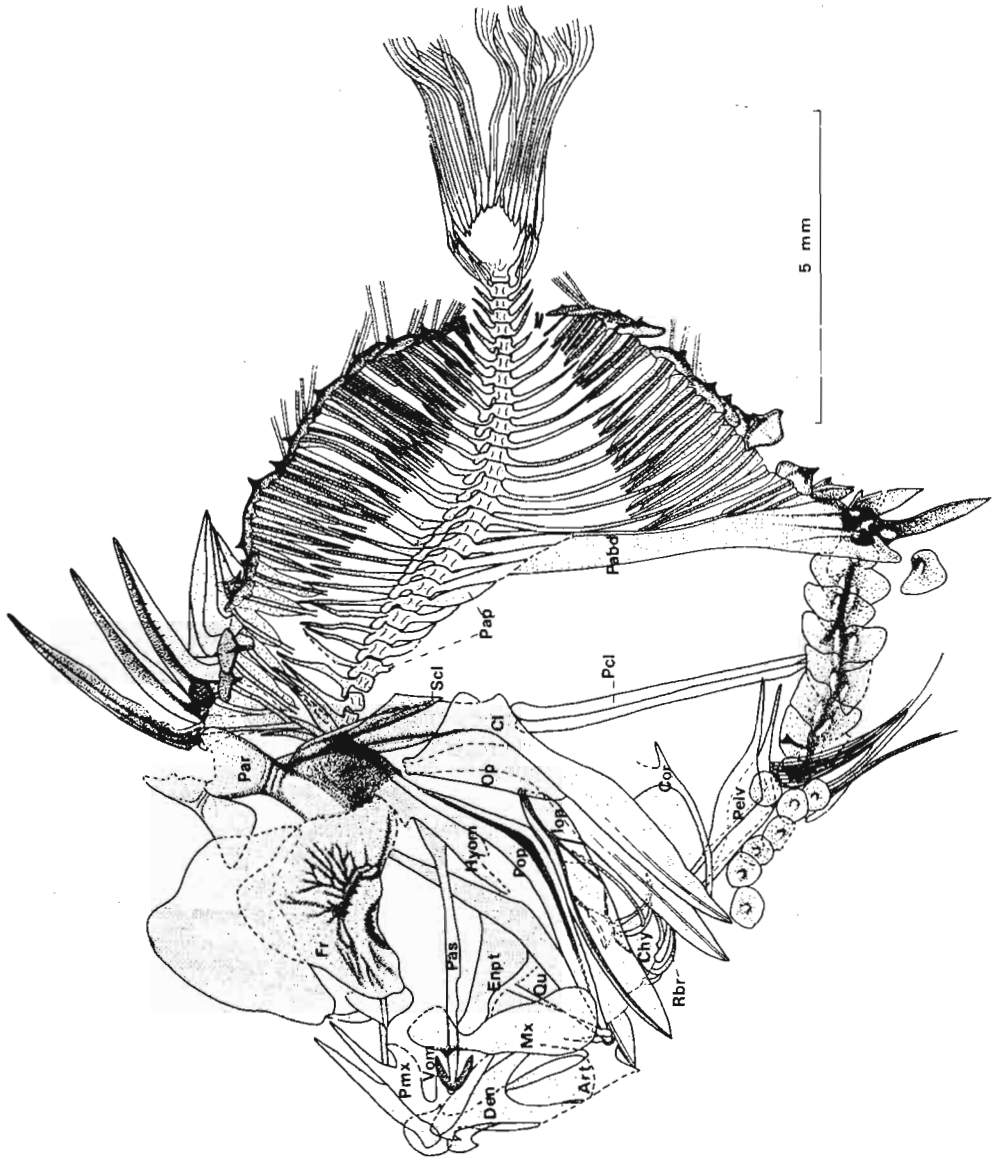


Fig. 5. *Zenopsis clarus* Daniltschenko, ZPALWr. A/2062, menilite shales, zone IPM 1, Jamna Dolna.

The oldest probable remains of a *Zenopsis* representative are from the Eocene in Georgia (Daniltshenko 1960: 90). In the younger Oligocene the genus was more common: fishes described by Kramberger (1891) and Paucă (1938) as *Zeus hörnesi*, and by Jonet (1958) as *Zeus aff. Hörnesi*, certainly should be assigned to *Zenopsis*.

This conclusion is based on the following data:

1. Kramberger described *Z. hoernesii* as a form with long caudal peduncle and long caudal skeleton section; the illustration shows (Kramberger 1891: pl. 4: 1) that there were 22 vertebrae (21 distinctly preserved, and remnants of hypural plates of the last vertebra).

2. The most important character of *Zenopsis* in the descriptions by Paucă (1938) and Jonet (1958) the presence of three spines in the anal fin. The latter mentions also the presence of bony bucklers below the spinous dorsal fin and the snout being perpendicular in front of the anterior orbit edge.

Lack of data as to the number of bucklers along the dorsal and the ventral body edge in *Zenopsis hoernesii* (Kramberger) makes it impossible to define relationship of this species to the fossil *Z. clarus*.

*Stratigraphic and geographic distribution.*— Early Oligocene: Caucasus, Polish Carpathians (Jamna Dolna).

### Family Caproidae, Lowe 1844

The oldest representative of the Caproidae is the extinct genus and species *Microcapros libanicus* Gayet from the Cenomanian in Liban (Gayet 1980 b).

The genus *Caprovesposus* Daniltshenko, included formerly within Caproidae, described from the Early Oligocene of the Caucasus (Daniltshenko 1960), was recently assigned to the family Caprovesposidae, order Perciformes (Bannikov and Fedotov 1984). The genera *Antigonia* and *Capros* occurred already in the Tertiary. The former is represented now by 5 species (Berry 1959) and is very rare in fossil record— so far only *Antigonia veronensis* Sorbini has been found in the Eocene of Monte Bolca (Sorbini 1983) and *Antigonia* sp. here described in the Oligocene of the Polish Carpathians (p. 130). Of the genus *Capros*, the only species living now, *C. aper*, has been known since the Miocene (Arambourg 1927). The stratigraphically oldest *C. rado-bojanus* appeared in the Early Oligocene and survived until the Miocene (p. 19). In the Late Oligocene of the Caucasus (Daniltshenko 1960) *C. longispinatus* Daniltshenko occurred, and in the Carpathians *C. medianus* sp. n. was found. Rückert-Ulkümen (1963) described from the Miocene of Turkey *C. breviventralis*. Judging from the illustrations (Rückert-Ulkümen 1963, 1965) the species does not belong to the genus *Capros*. The characters of *C. longispinatus* have been given after Prof. Jerzmańska's personal communication.

### THE KEY TO THE SPECIES

- 1 a. The upper branch of cleithrum with or without ridges, anterior angle of the supraoccipital crest on the line of the posterior orbit edge; operculum with a deep notch in the upper section; in the anal fin the first spine is the longest; thirteen caudal vertebrae . . . . . 2
- 1 b. The upper branch of cleithrum with ridges; anterior angle of the supraoccipital crest is not on the line of the posterior orbit edge; operculum with a shallow notch in the upper section; in the anal fin the second spine is the longest; twelve caudal vertebrae . . . . . 3

- 2 a. The upper branch of cleithrum without ridges; the length of the third spine of the dorsal fin equal to the maximum body depth . . . . *Capros radobojanus*  
 2 b. The upper branch of cleithrum with ridges; the length of the third spine 1.5 times larger than the maximum body length . . . . *Capros longispinatus*  
 3 a. Anterior angle of the supraoccipital crest in front the line of the posterior orbit edge; in the dorsal fin the second spine shorter than the subsequent ones; 3.5 vertebrae in the caudal peduncle . . . . *Capros medianus*  
 3 b. Anterior angle of the supraoccipital crest is on the central line of the orbit; in the dorsal fin the second spine is longer than the two last ones; 1—2 vertebrae in the caudal peduncle . . . . *Capros aper*

Genus *Capros* Lacépède, 1802

*Capros radobojanus* (Kramberger, 1882)

(figs. 6, 10)

1960. *Capros radobojanus* (Kramberger, 1882); Daniltshenko: 92, pl. 9: 1; fig. 19.

1968. *Capros radobojanus* (Kramberger, 1882); Jerzmańska: 443; pl. 5: 2; fig. 17.

Formula: D-IX/22; A-III/22; P-15; V-I-5; Vert. 10+13 = 23.

**Material.**—Two imprints (ZPALWr. A/2072—2073) from Przysietnica and thirty eight specimens from the collection of A. Jerzmańska (1968).

**Description.**—Characters of this species given by Jerzmańska (1968) were supplemented by the following data.

**Skull.** On the frontal there are traces of serrate bony ridges situated radially. Supraoccipital crest starts above the posterior orbit edge, in adults its edge is smooth. Serration of anterior edge of supraoccipital crest, given by Jerzmańska (1968) occurs only in juvenile specimens, which reach 1.5 cm of standard length (fig. 6). The articular process of premaxilla is shorter than its horizontal section, and forms a clear convexity below the cusp of the ascending process of this bone (fig. 6). The shoulder girdle is well-preserved; cleithrum has smooth surface, no traces of bony ridges (fig. 10).

**Anal fin.** The first spine is the longest and the strongest. The distance between the last rays of the dorsal and the anal fins and the base of the caudal fin rays corresponds to the length of the last three or three and a half vertebrae.

**Remarks.**—A characteristic feature of the specimens of *C. radobojanus* is the strong skeleton of relatively thick bones and strong scales with traces of 5 to 12 short spines. The above-mentioned serrulate edge of the supraoccipital crest in *C. radobojanus* remind the serrate bone ridges, which in Recent *C. aper* occur on skull bones both in juvenile and adult specimens. *C. radobojanus* is different from *C. aper* in the premaxilla structure. In *C. aper*, in contrast to *C. radobojanus*, the articular process is fused with the ascending process, and both processes are far longer than the horizontal section of the premaxilla.

Several new fossil genera and species of Caproidae described by Kramberger (1882) and Cosmovici (1887) from the Oligocene and Miocene in Europe, were considered by Weiler (1928) to be representatives of the genus *Capros*. Paučá (1934) reduced the number of species to two: *Capros radobojanus* and *C. longirostris*. He stressed, however, that the only differences found in body shape may result from individual variability within one species. Daniltshenko (1960) and Jerzmańska (1968) regarded *C. longirostris* to be a synonym of *C. radobojanus*. All the same Andelkovič (1976) and Ciobanu (1977), without considering earlier views, quote both species separately. The analysis of descriptions and illustrations in Paučá's paper (1934) and the studied

material confirm the views of Daniltshenko (1960) and Jerzmańska (1968) that *C. longirostris* is a synonym of *C. radobojanus*.

*Stratigraphic and geographic distribution.*— Miocene: Croatia, Serbia. Oligocene: F. R. G., Romania, Poland (Carpathians).

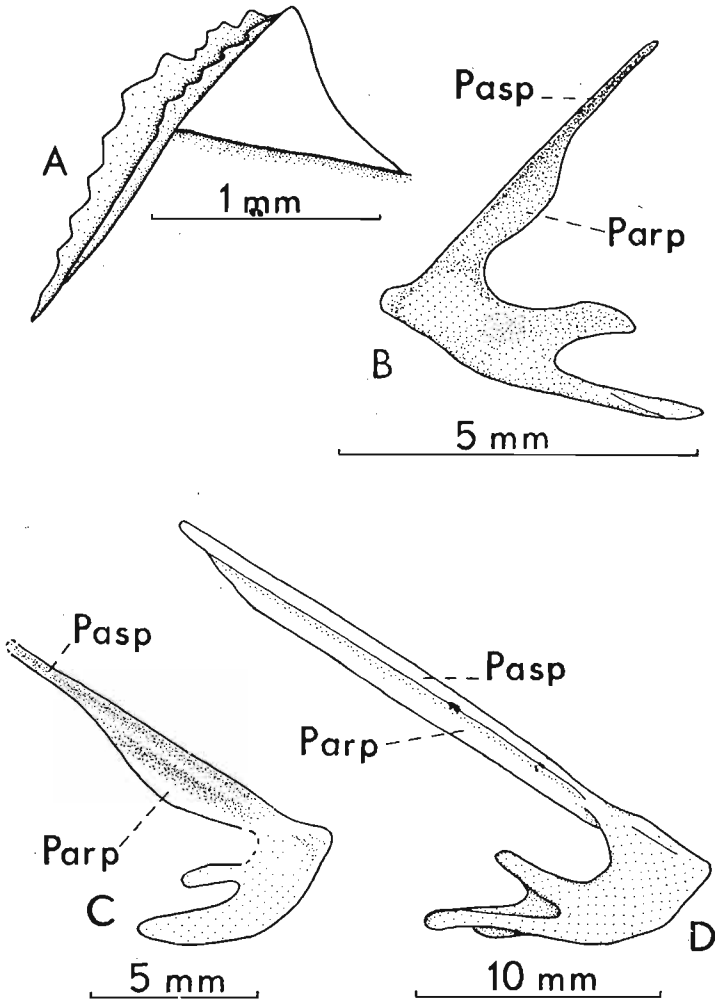


Fig. 6. **A** *Capros radobojanus* (Kramberger), ZPALWr. A/1783, supraoccipital crest serration, menilite shales, zone IPM 2, Rogi; **B** *Capros radobojanus* (Kramberger), ZPALWr. A/913, right premaxilla from inside, menilite shales, zone IPM 2, Rogi; **C** *Capros medianus* sp. n., ZPALWr. A/2059, left premaxilla from inside, menilite shales, zone IPM 6, Błażowa Rzeszowska; **D** *Capros aper*, right premaxilla of contemporary specimen from outside.

*Capros medianus* sp. n.

(pl. 47, 48; figs. 6—10)

*Holotype*: imprint of the anterior body part ZPALWr. A/2059; pl. 47 and figs. 6—8, and 10.

✓ *Type horizon*: Oligocene, zone IPM 6 of the Menilite Beds.

*Type locality*: Błażowa Rzeszowska.

*Derivation of the name:* Lat. *medianus*—intermediate, species having some characters of *C. aper* and *C. radobojanus*.

*Diagnosis.*—Anterior angle of the supraoccipital crest in front of the line of the posterior orbit edge, in the dorsal fin 9 spines, the 2nd shorter than all the subsequent ones, and 18 rays; in the anal fin there are 3 spines, the 2nd is the longest, and 18 rays; operculum has a shallow notch in the upper section; scales are thin, with numerous bristly spines.

Formula: D-IX/18; A-III/18; V-I/5; Vert. 10+12 = 22; C-3+12+3.

*Material.*—Three incomplete imprints from the site Błazowa Rzeszowska (ZPALWr. A/2058—2060).

Dimensions in mm:

	A/ZPALWr.:		
	2058	2059	2060
maximum body depth	14.4	31.7	—
body depth at anal fin beginning	11.7	—	26.8
head length	11.2	21.9	—
pre-dorsal length	12.8	23.6	—
orbit diameter	3.6	7.4	—
pre-anal length	17.1	—	—
I anal fin spine length	2.4	5.4	6.4
II anal fin spine length	2.6	5.7	6.9
III dorsal fin spine length	8.4	18.4	21.8

*Description.*—**Skull** (fig. 7). Head is shorter than the maximum body depth. Neurocranium short, frontals widened posteriorly and have traces of serrulate bone ridges (fig. 7); high supraoccipital crest starts before the line of the posterior orbit edge, its anterior edge is very strong; the blade of the crest posteriorly provided with a notch (fig. 7), horizontal orbit diameter is 1/3 of the head length. The articular process of premaxilla is elongate, marked by small convexity on the posterior edge of the longer ascending process (figs. 6—7). Preoperculum large, hooked at right angle, at the angle region traces of thick bone ridges occur (figs. 7, 8), which protrude beyond the edge of this bone in the form of spines. Operculum small, subtriangular, the upper section well-developed with a shallow notch (figs. 7, 8); suboperculum and interoperculum invisible.

**Vertebral column.** First abdominal vertebra without ribs, well-developed parapophyses visible only on four last abdominal vertebrae; of nine rib pairs especially strong are those on the penultimate abdominal vertebra which contact with their lower ends the first pterygiophore of the anal fin; the ninth rib pair is very short and delicate (fig. 9). The haemal spine of the first caudal vertebra forms the upper section of the postabdominal. In the caudal peduncle, preserved only in one specimen, there are 3.5 last caudal vertebrae.

**Dorsal fin.** Nine strong spines in the spinous fin, in the soft fin 18 rays, covered on both sides with minute, bristly spines (fig. 9). The third spine of the dorsal fin is smaller than the maximum body depth, the second is shorter than all the subsequent ones (figs. 7, 9). The beginning of the fin is on the vertical line of the posterior operculum edge. The last pterygiophore lies above the 9th caudal vertebra.

**Anal fin.** Of the three strong spines the second is the longest. The first spine is on the line of the ninth spine of the dorsal fin, in the soft there are 18 rays, covered on both sides with minute spines. Two large first pterygiophores form the lower section of the postabdominal (fig. 9). The last interhaemal spine lies under the 9th caudal vertebra.

**Caudal fin.** Eighteen rays, including 12 principal rays (fig. 9). The skeleton of the caudal fin has no clear differences in comparison to Recent *Capros aper*.

**Pectoral fins.** Poorly preserved. In the shoulder girdle the cleithrum is well-developed, the upper branch is smaller, covered with serrulate bone ridges (figs. 7, 10), the lower branch is far bigger, distally widening, fusing with the pelvic girdle

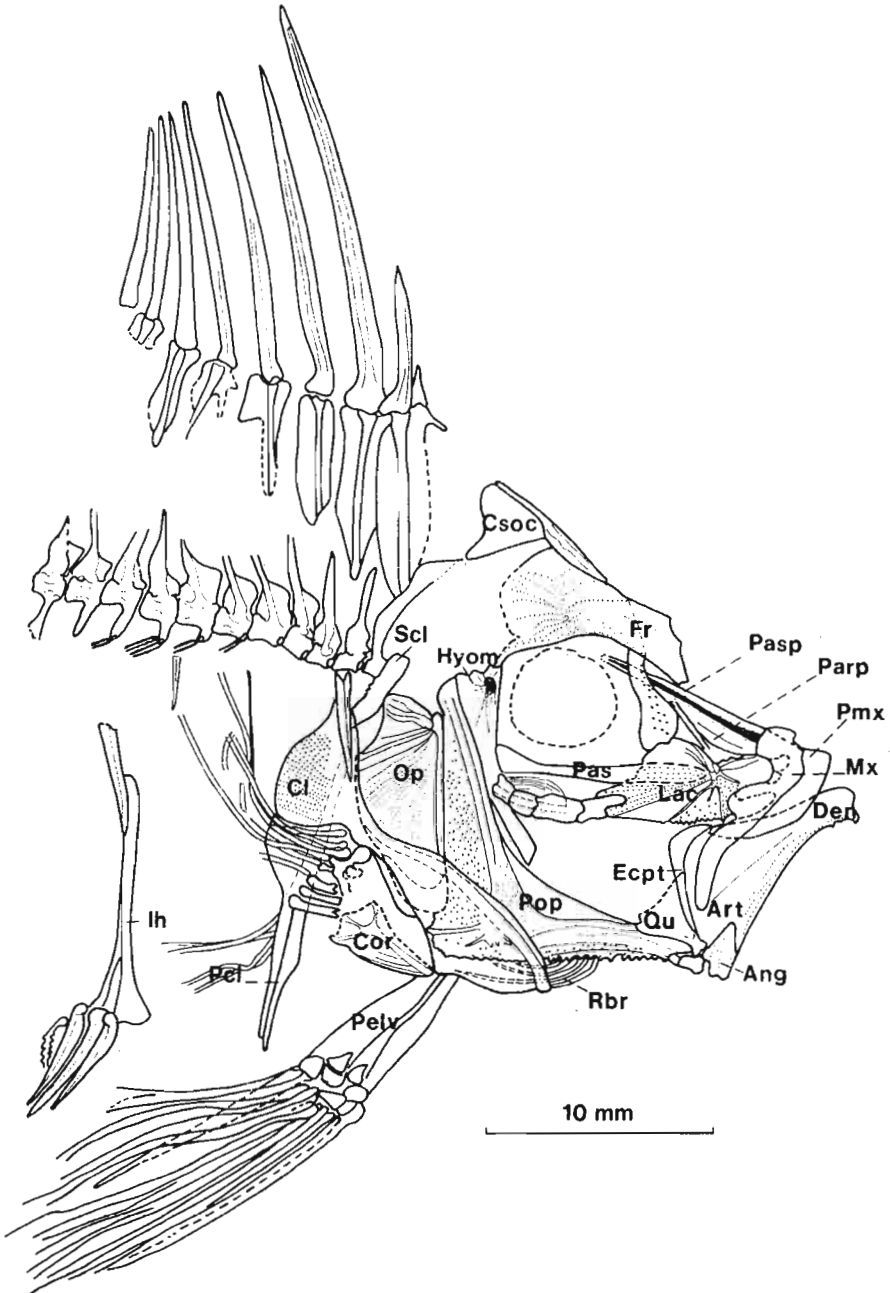


Fig. 7. *Capros medianus* sp. n., ZPALWr. A/2059, anterior body part, menilite shales, zone IPM 6, Białowa Rzeszowska.



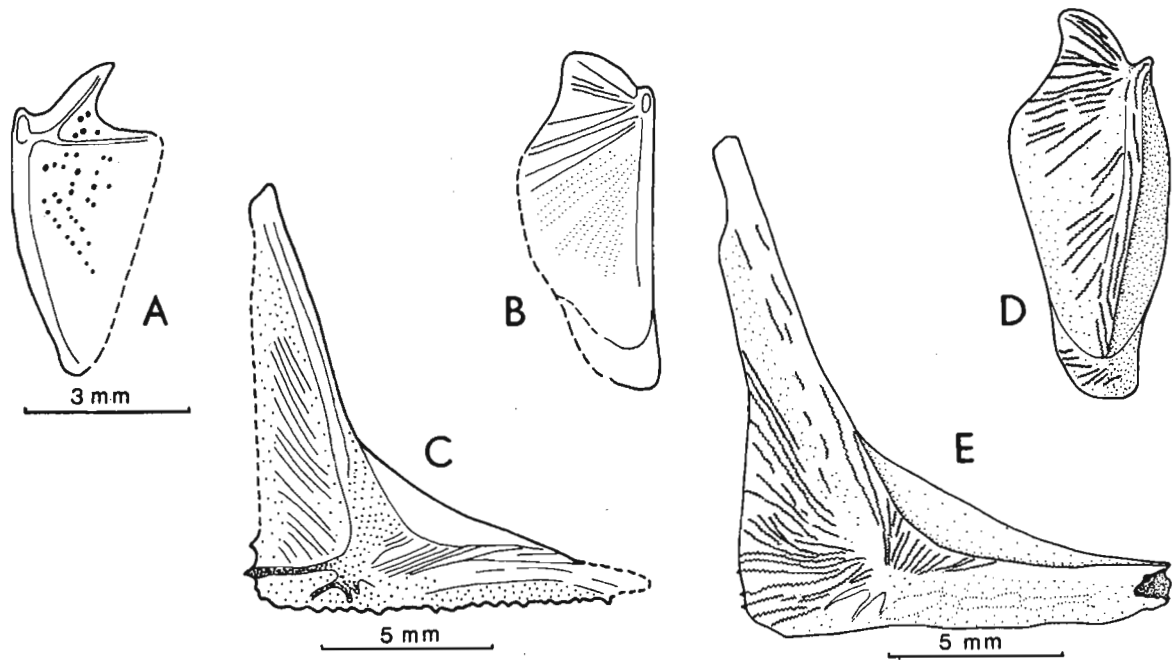


Fig. 8. **A** *Capros radobojanus* (Kramberger), ZPALWr. A/1786, right operculum, external surface imprint, zone IPM 2, Rogi; **B, C** *Capros medianus* sp. n., ZPALWr. A/2059, left operculum preoperculum, external surface imprint, menilite shales, zone IPM 6, Błażowa Rzeszowska; **D, E** *Capros aper*, right operculum and preoperculum of Recent specimen from outside.

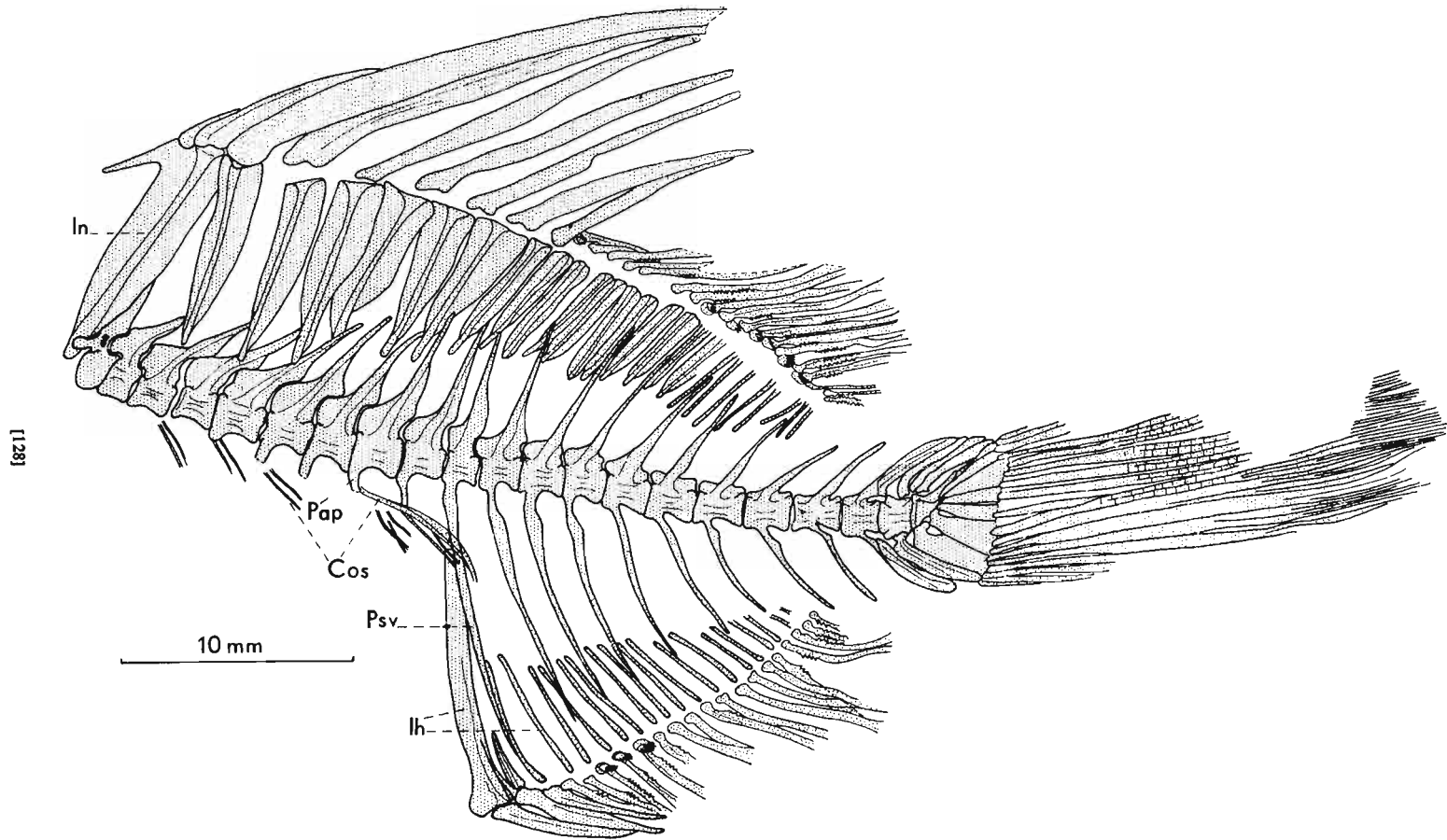


Fig. 9. *Capros medianus* sp. n., ZPALWr. A/2060, backbone and unpaired fins, menilite shales, zone IPM 6, Błazowa Rzeszowska.

(fig. 7); post-cleithrum is bayonet-shaped, strongly posterad, not reaching the ventral edge (fig. 7).

**Pelvic fins.** In each one strong spine is shorter than the rays. The pelvic girdle is large and strong (fig. 7).

Scales are small and very delicate, posteriorly with numerous bristly spines. On some scales about 30 spines. Scales form a compact squamation which occasionally obscures the outline of bones.

**Remarks.**—Recent Caproidae (*Capros* and *Antigonina*) have only 22 vertebrae (Rosen 1984). Among fossil species of the genus *Capros* there were two forms, C.

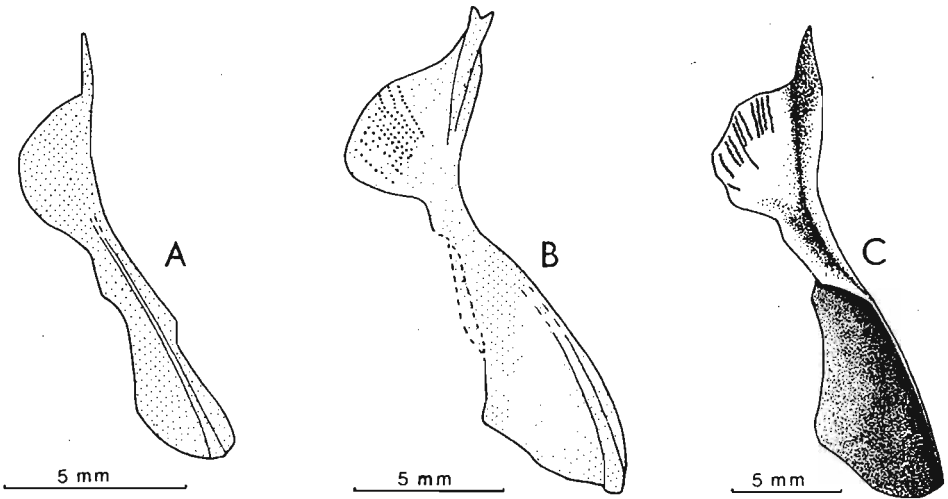


Fig. 10. **A** *Capros radobojanus* (Kramberger), ZPALWr. A/1779, left cleithrum, internal side, menilite shales, zone IPM 2, Rogi; **B** *Capros medianus* sp. n., ZPALWr. A/2059, left cleithrum, internal side, menilite shales, zone IPM 6, Błażowa Rzeszowska; **C** *Capros aper*, right cleithrum of Recent specimen, external side.

Table 3

Osteological similarities and differences in three species of the genus *Capros*

No.	Character	<i>C. radobojanus</i>	<i>C. medians</i>	<i>C. aper</i>
1	Caudal vertebrae counts	13	12	12
2	Caudal peduncle	long	long	short
3	Dorsal fin end above caudal vertebra	10	9	10
4	Anal fin end below caudal vertebra	10	9	10
5	Notch in operculum posterior edge	deep	shallow	shallow
6	Ridges on cleithrum	none	present	present
7	The longest spine in anal fin	first	second	second

*radobojanus* and *C. longispinatus*, with 23 vertebrae and *C. medianus* and *C. aper* with 22 vertebrae. In the evolution of the genus *Capros* the abdominal section of the backbone does not change (always 10 abdominal vertebrae), the backbone shortens in the caudal section only in *C. medianus* and *C. aper*. Further changes in the caudal body section in three better known species of *Capros* (cf. table 3) concern development of soft dorsal and anal fins and the length of the caudal peduncle. In *C. medianus* the shortening of the caudal section of the backbone is accompanied by shortening of the bases of soft dorsal and anal fins and by decrease in the number of soft rays by the long caudal peduncle. Another tendency can be seen in *C. aper* in which, though the caudal section of the backbone is shortened, the number of the soft rays in dorsal and anal fins increased, the bases of the fins having the same length (cf. table 3, character 3, 4). As a result dorsal and anal fin pterygiophores are cramped in *C. aper*. For instance in the anal fin the number of pterygiophores between I and II haemal spine in the studied specimens of *C. aper* is 4, in *C. medianus* and *C. radobojanus* there are only three. In the dorsal fin in *C. aper* a similar cramping can be seen e.g. above the seventh caudal vertebra. These characters (including also structure of premaxilla, operculum, cleithrum, proportion of spines in dorsal and anal fin) in the three *Capros* species seem to suggest that both *C. medianus* and *C. aper* could have a common ancestor, close to *C. radobojanus*. In the Polish Carpathians the latter was found in zones IPM 2, IPM 4, and occasionally young individuals in zone IPM 1. Until now *C. medianus* has been found only in zone IPM 6. In the Caucasus *C. longispinatus* (Daniltshenko 1960) occurs in the Riki horizon sediments (Late Oligocene), which correspond to layers of the zone IPM 6 in the Carpathians (Jerzmańska, Kotlarczyk in print). *C. medianus*, in contrast to *C. longispinatus* (p. 123), has a lower supraoccipital crest, a different shape of upper operculum section, third spine of the dorsal fin shorter than maximum body depth, longer second spine in the anal fin and lower number of caudal vertebrae. Both forms are similar in having ridges on the upper cleithrum branch.

*Stratigraphic and geographic distribution.* — Late Oligocene: Polish Carpathians (Błazowa Rzeszowska).

### Genus *Antigonia* Lowe, 1843

#### *Antigonia* sp.

(pl. 49; fig. 11)

*Material.* — One bilateral skull imprint and a fragment of dorsal fin (ZPALWr. A/2074).

*Site.* — Przysietnica.

*Dimensions* in mm:

	ZPALWr.	A/2074
head length		12.1
head depth		17.3
supraoccipital crest height		3.5

*Description.* — Imprints of external body surface, visible in the specimen from inside, are shown in fig. 11. The head length may suggest that the whole specimen was c. 30 mm in standard length.

*Skull.* Head profile very steep. Supraoccipital crest very high and steep, anterior edge strong, anterior crest angle on the middle orbit line. On the frontal (posteriorly considerably widened) there are imprints of serrate ridges from the external surface of the bone. Nasal large, slightly curved. Parasphenoid strong, posteriorly bent up-

wards. In the palatine, the dorsal fragment of the posterior section connected to the large entopterygoid is visible. In the metapterygoid, only the upper section connecting with the hyomandibular is visible. The ectopterygoid, triangular in shape, connected to the quadrate. In the symplectic, the part connecting with the quadrate is visible. The lachrymal very large, intensely ornamented. Snout small, premaxilla not large. Mandible high. Operculum elongate vertically, with a notch in the upper section; in the lower section the subopercular profile is visible. Praeoperculum very large, bent at right angle; imprints of serrate bone ridges from the external surface of the bone

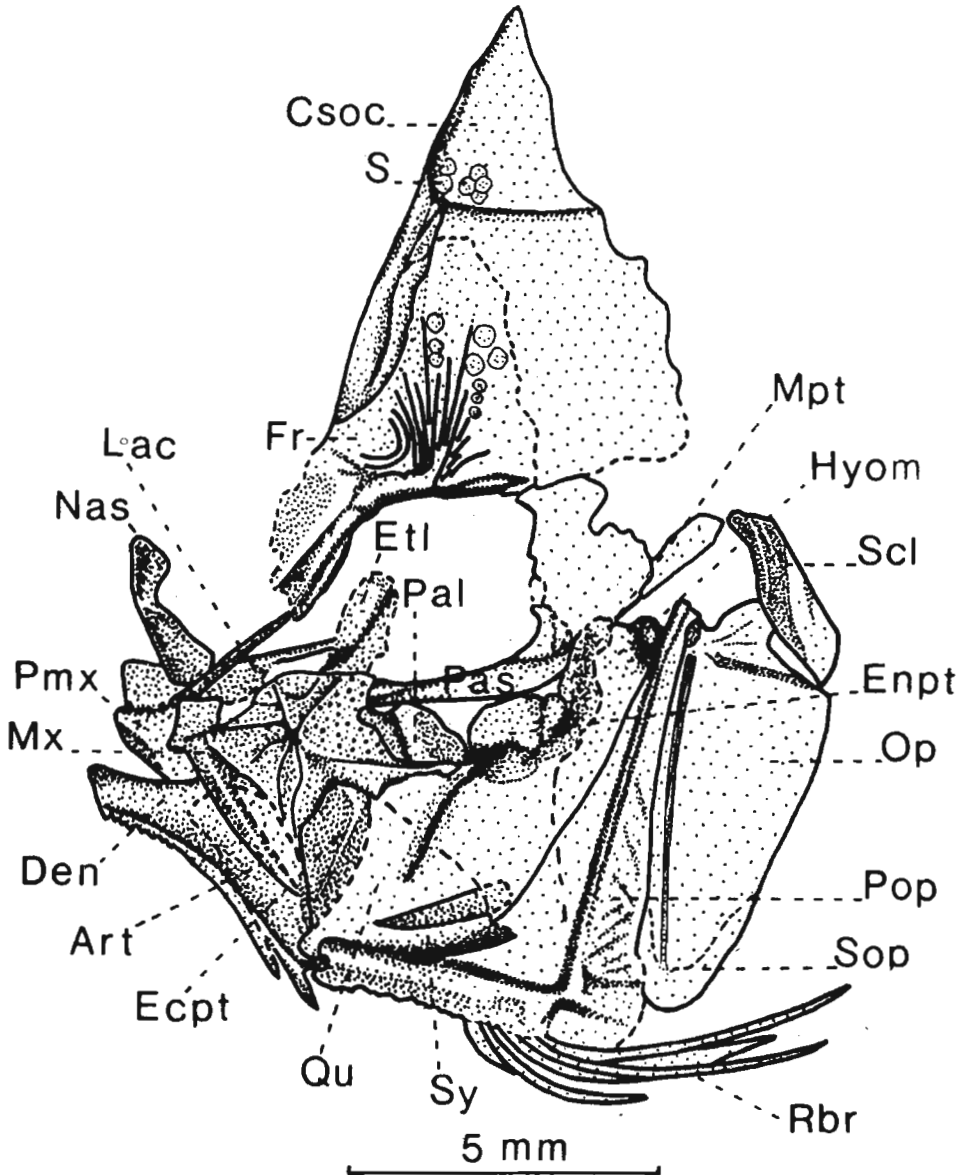


Fig. 11. *Antigonía* sp., ZPALWr. A/2074, imprint of external surface of skull bones, menilite shales, zone IPM 4, Przysietnica.

can be seen. Five branchiostegal rays, sabre-shaped, can be seen. Above the operculum the supracleithrum is visible. Traces of minute roundish scales covered with spines show that the scales covered the larger part of the head.

*Remarks.*—The described skull is generally similar to living species *Antigonia capros*, but is different in structure of operculum and preoperculum and in shape of scales.

On the same piece of rock, below the skull, a fragment of the spinous dorsal fin can be seen, consisting of 5 spines with partly preserved pterygiophores. The first of the spines is the smallest, contacting the anterior edge of the second spine which, though partly damaged, is longer and stronger than the following ones.

Scarcity of available material makes it impossible to carry out more detailed comparisons with 5 living species of the genus *Antigonia* (Berry 1959) and with the oldest species—*Antigonia veronensis* Sorbini from the Eocene of Monte Bolca (Sorbini 1983). In the Oligocene of the Carpathians the genus *Antigonia* was found for the first time. It was the second finding of this genus in fossil state. Otoliths of the genus *Antigonia* are known from the middle Miocene of F. R. G., Romania, Portugal (Jonet 1972—1973), Poland, Slovakia (Šmigielska 1979), Belgium, France (Steurbaut 1984) and the Early Miocene of France (Steurbaut 1984).

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JACEK ŚWIDNICKI

## OLIGOCENSKIE ZEIFORMES (TELEOSTEI) Z KARPAT POLSKICH

### Streszczenie

Opracowano osteologię kopalnych Zeiformes i przedstawiono ich rozmieszczenie w zonach ichtiofaunistycznych (tabela 1) zgodnie z podziałem podanym przez Kotlarczyka i Jerzmańską (1976). Stwierdzono po raz pierwszy w Karpatach rodzaj *Antigonia* (Caproidae) oraz *Zeus faber* (Zeidae). W stanie kopalnym jest to drugie występowanie przedstawiciela rodzaju *Antigonia*, obok *Antigonia veronensis* Sorbini znanego ze środkowego eocenu Monte Bolca (Sorbini 1983). Zestawiono cechy diagnostyczne (tabela 2) dla rodzajów *Zeus* i *Zenopsis* (Zeidae). Ustalono, że *Zenopsis* sp. z Karpat jest synonimem kaukaskiego gatunku *Zenopsis clarus* Daniltshenko. Wykazano, że cechy osteologiczne *Zeus hoernesii* upoważniają do przeniesienia tej formy do rodzaju *Zenopsis*. Sporządzono klucz do oznaczania gatunków rodzaju *Capros*. Opisano nowy gatunek *Capros medianus*, który różni się cechami osteologicznymi od pokrewnych gatunków *C. radobojanus* i *C. aper*. Wydaje się, że *C. medianus* nie był przodkiem *C. aper*, natomiast oba te gatunki mogły powstać z formy bliskiej *C. radobojanus*.

Praca została wykonana w ramach problemu M.R.II/6.

## EXPLANATION OF PLATES 47—50

### Plate 47

*Capros medianus* sp. n., Oligocene, zone IPM 6, Błazowa Rzeszowska: holotype, ZPALWr. A/2059, anterior body part, left side, ca. ×3.



## Plate 48

*Capros medianus* sp. n., Oligocene, zone IPM 6, Białowa Rzeszowska: ZPALWr. A/2060, backbone and unpaired fins, left side, ca.  $\times 3$ .

## Plate 49

*Antigonia* sp., Oligocene, zone IPM 4, Przysietnica: ZPALWr. A/2074, skull, right side, ca.  $\times 9$ .

## Plate 50

1. *Antigonia* sp., Oligocene, zone IPM 4, Przysietnica: ZPALWr. A/2074, fragment of dorsal fin, right side; 2ab. *Zeus faber*, Oligocene, zone IPM 5, Krępak: ZPALWr. A/2066, scales SEM.

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