www.czasopisma.pan.pl PAN POLSKA AKADEMIA NAUK www.journals.pan.pl

Acta Geologica Polonica, Vol. 74 (2024), No. 1, e5

DOI: 10.24425/agp.2023.148029

A new clupeoid genus from the Oligocene of Central Paratethys (Menilite Formation, Poland)

MATEUSZ GRANICA[1], MAŁGORZATA BIEŃKOWSKA-WASILUK[1] and MARCIN PAŁDYNA[2]

[1] *University of Warsaw, Faculty of Geology, Żwirki i Wigury 93, 02-089 Warszawa, Poland;*
e-mails: m.granica2@uw.edu.pl; m. wasiluk@uw.edu.pl
[2] *e-mail: mar.dyna@wp.pl*

ABSTRACT:

Granica, M., Bieńkowska-Wasiluk, M. and Pałdyna, M. 2024. A new clupeoid genus from the Oligocene of Central Paratethys (Menilite Formation, Poland). *Acta Geologica Polonica*, **74** (1), e5.

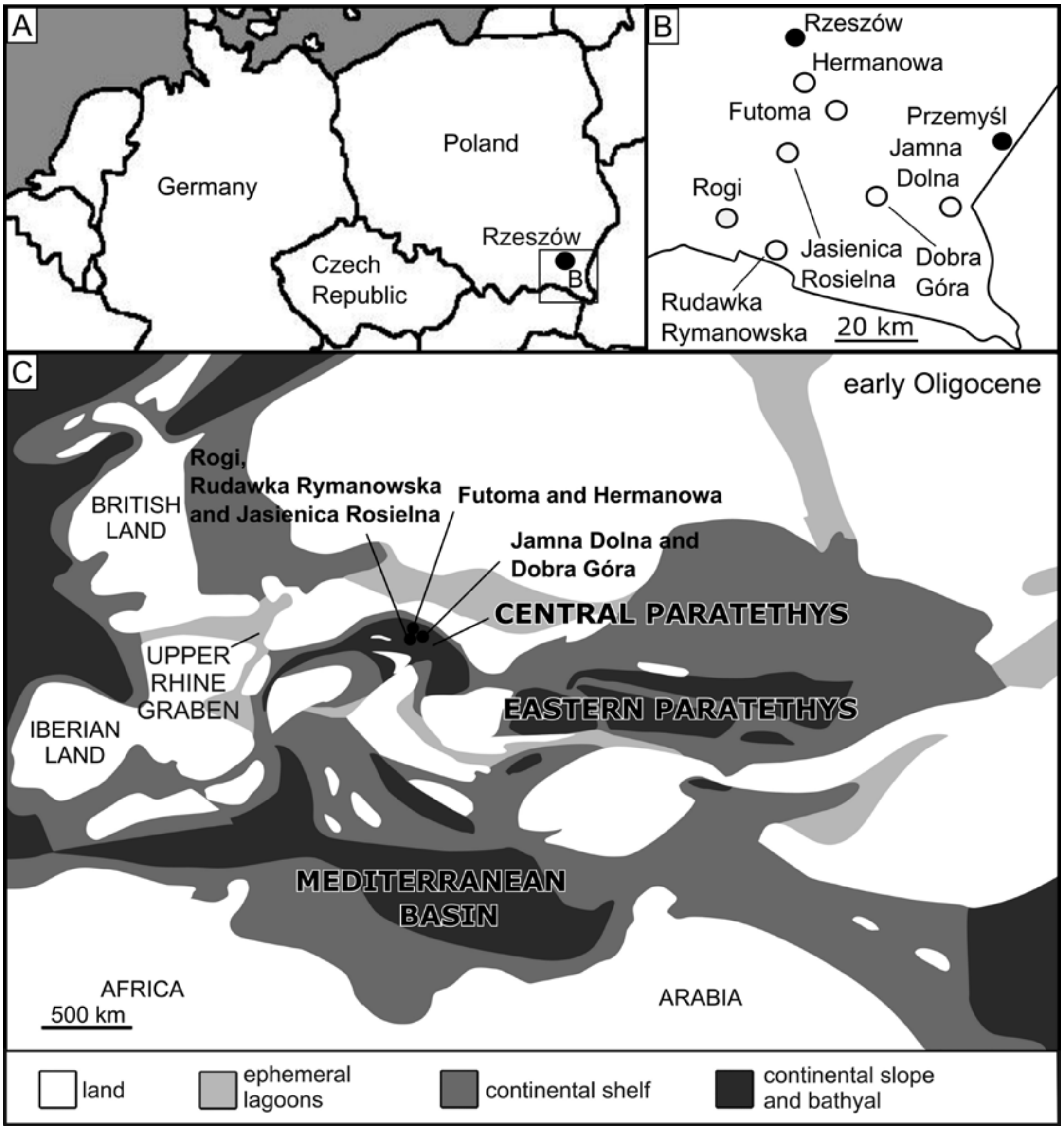
The Suborder Clupeoidei Bleeker, 1859 comprises mostly marine fishes, which form large schools feeding on plankton. The fossil record of the suborder in the Late Paleogene reveals that clupeoids were abundant in the Western, Central, as well as Eastern Paratethys. Clupeoid descriptions from the Polish Outer Carpathians (SE Poland, Central Paratethys) remain incomplete due to usage of 'collective species', taxonomical inaccuracies, and lack of clear links between extinct and extant representatives. In this paper we present a new clupeoid, †*Beksinskiella* gen. nov., from the Oligocene of the Outer Carpathians, Poland. The new genus encompasses the nominal species †*Maicopiella longimana* (Heckel, 1850). †*Beksinskiella* gen. nov. has a unique combination of characters (skull roof with frontoparietal striae; smooth opercle; 6–7 branchiostegal rays; 42–48 vertebrae; dorsal and anal fins with 21–23 rays; the last two rays of the anal fin being elongated, and the presence of a complete series of abdominal scutes with the postpelvic ones poorly developed), supporting recognition of a new genus of the Suborder Clupeoidei. Similarities and differences between fossil and extant genera of Cluepoidei are discussed to shed light on their relationship.

Key words: Clupeiformes; †*Beksinskiella* gen. nov.; Paratethys; Oligocene; Menilite Formation; Poland.

https://zoobank.org/References/e31ded87-a7dd-4040-8980-a31ad08c53c1

INTRODUCTION

The Suborder Clupeoidei Bleeker, 1859 is part of the Order Clupeiformes Bleeker, 1859, one of the most widespread and abundant group among the teleosts. This suborder consists of anchovies, herrings, shads, sardines, hilsa, and menhadens. They form large schools and occupy mostly marine and brackish environments, although some species also inhabit fresh water (Nelson *et al.* 2016). The first fossil record of the Clupeoidei can be traced back to the Early Cretaceous (Figueiredo 2009). The systematics of extinct clupeoids is still far from being fully understood (Grande 1985; Lavoué *et al.* 2014; Wang *et al.* 2022). The diagnostic features and phylogeny of extant clupeoids are complex and still under debate (Whitehead 1985; Lavoué *et al.* 2013, 2014; Wang *et al.* 2022). Taxonomic problems regarding Clupeoidei fishes are a result of e.g., incomplete description of the osteology or usage of 'collective species', which put several different taxa within the synonymy of a single species, as commented on †*Sardinella sardinites* (Heckel, 1850) by Pharisat and Micklich (1998), and described by Kovalchuk *et al.* (2020). †*Sardinella sardinites* (Heckel, 1850) is a prime example of such complexity and 'collective species'; it has been treated as a species



Text-fig. 1. Location map of the study area. A – Study area within Central Europe; B – Localities where specimens were collected (black dots); C – Early Oligocene (Rupelian) palaeogeography (modified from Popov *et al*. 2002) with the location of the fossil sites.

with a wide stratigraphic range from the Oligocene to the Miocene, and with a palaeobiogeographic occurrence from the Western to the Eastern Paratethys (see e.g., Popov *et al.* 2002; Maxwell *et al*. 2016). A second example of such a problematic taxon is *Pomolobus* Rafinesque, 1820. This genus is currently considered a junior synonym of *Alosa* Linck, 1790. †*Pomolobus antiquus* (Smirnov, 1936), †*P. curtus* Daniltshenko, 1960 and †*P. facilis* Daniltshenko, 1960 have been described from the Oligocene. Several diagnostic characters of the Alosidae Svetovidov, 1952 are evident in these species but they differ in having a significantly lower number of vertebrae from the species of the genus *Alosa*. Therefore these three Oligocene species are regarded in this paper as †‘*Pomolobus*’ Rafinesque, 1820. The diagnostic features used in extant genera and species include mostly soft tissue data (see Whitehead 1985) that are usually not preserved in the fossil record. Thus, the group is difficult to understand and describe (Baykina 2012, 2013a, b; Přikryl *et al*. 2016). Intense studies of the ichthyofauna of the Polish Outer Carpathians have been conducted since the 1950s (e.g., Jerzmańska 1958, 1960, 1968, 1979; Kotlarczyk and Jerzmańska 1988; Kotlarczyk *et* *al*. 2006) providing us with detailed palaeontological, sedimentological and lithostratigraphic data. Although the clupeoids represent an abundant fish group in the Polish Outer Carpathians, many specimens were described merely as Clupeidae indet. The monophyly of this family is, however, contested (Li and Ortí 2007; Lavoué *et al*. 2013, 2014; Wang *et al*. 2022). This was the starting point for the recent reviews by Přikryl *et al*. (2016) and Kovalchuk *et al*. (2020). Our study is a follow-up to the ichthyofaunal studies conducted on material from the Polish Outer Carpathians. We describe a new genus of clupeoid fish based on material (see Appendix 1) housed at the University of Warsaw. We provide an osteological description that has allowed us to infer the presence of a new genus, providing at the same time a new hypothesis about the taxonomic status of †*Maicopiella longimana* (Heckel, 1850) from deposits of the Carpathian Basin in the Central Paratethys (Text-fig. 1). Specimens with a similar morphology to those from Poland have in the past been usually assigned to †*Clupea sardinites* (Heckel, 1850) (see e.g., Jerzmańska 1968; Kotlarczyk *et al*. 2006). Many clupeoid fishes of the Paratethys were traditionally described as †*Clupea sardinites* or †*Sardinella sardinites.* Our literature review indicates that specimens assigned to this species from different localities in Europe should be revised to verify their taxonomic position. For example, osteological data about some bones (frontal, opercle, preopercle, branchiostegal rays, etc.) which are important for interpretation, are insufficiently presented in older reports. Furthermore, we present comparisons of the studied specimens with extant and extinct members of the Suborder Clupeoidei. We consider our study to represent a further step towards a better understanding of clupeoid biodiversity in the Oligocene of Central Paratethys.

GEOLOGICAL SETTING

The collected material comes from the Podkarpackie Voivodeship, with Rzeszów, Przemyśl, and Sanok being the main cities in this region. The specimens were found in the Dobra Góra, Futoma, Hermanowa, Jamna Dolna, Jasienica Rosielna, Rogi, and Rudawka Rymanowska localities in the Polish Outer Carpathians (Text-fig. 1B). The material was collected from the Menilite Formation (Kotlarczyk *et al.* 2006) in the Skole and Silesian tectonic units. The Menilite Formation is usually represented by brownish-black, usually non-calcareous shales. The formation is laterally interbedded with the ash-grey, strongly calcareous, and micaceous sandstones and shales of the Krosno Formation. Both formations constitute the Menilite-Krosno Series (Kotlarczyk *et al.* 2006). The Futoma (Błażowa) locality (Bieńkowska-Wasiluk and Pałdyna 2018) lies 20 km south-east of Rzeszów, in the Skole Unit. The specimens from this locality come from the Futoma Diatomite Member, from ichthyofaunal zone IPM2. The Hermanowa locality (Kotlarczyk *et al.* 2006; Přikryl *et al.* 2016) is situated 10 km south of Rzeszów, the Dobra Góra locality (Kotlarczyk *et al.* 2006) is located 15 km north-east of Sanok, and the Jamna Dolna locality (Kotlarczyk *et al.* 2006; Bieńkowska-Wasiluk 2010) – 20 km south-west of Przemyśl. In these three localities of the Skole Unit the specimens were obtained from the Rudawka Tractionite Member Unit, in ichthyofaunal zone IPM2. The Jasienica Rosielna locality (Wasiluk 2013) is situated 30 km south of Rzeszów, and the Rogi locality (Kotlarczyk *et al.* 2006) lies 50 km south-west of Rzeszów. In these two localities of the Silesian Unit the specimens come from the upper part of the Menilite Formation, from ichthyofaunal zone IMP2. The Rudawka Rymanowska locality (Bieńkowska 2004; Kotlarczyk *et al.* 2006) is located 55 km south of Rzeszów in the Silesian Unit. Here, the specimens were collected from the Tylawa Limestones, from ichthyofaunal zone IPM2. All described specimens are Early Oligocene (Rupelian) in age. Ichthyofaunal zone IPM2 is correlated with the calcareous nannoplankton biozone NP23 (Kotlarczyk *et al.* 2006).

MATERIAL AND METHODS

The material is housed in the Stanisław Józef Thugutt Geological Museum (MWGUW) of the Faculty of Geology, University of Warsaw, and consists of 39 complete and nearly complete articulated skeletons (Text-fig. 2). The specimens were collected between 1995 and 2017 by faculty members and their collaborators. The material was examined using a Nikon SMZ 1000 stereomicroscope. Photographs were taken using the stereomicroscope equipped with a digital camera using the DLT cam viewer software. Observations and photographs were conducted in the Scanning Electron and Optical Microscopy Laboratory at the Faculty of Geology, University of Warsaw.

All fish measurements were standardised based on standard length (SL). The osteological terminology follows Grande (1985), and Whitehead and Teugels (1985). Comparative information was derived from the literature (Daniltshenko 1960, 1980; Grande 1985; Whitehead 1985; Murray *et al.* 2005; Baykina

2012, 2013a; Marramà and Carnevale 2015a, b, 2018; Baykina and Schwarzhans 2017a, b; Kevrekidis *et al.* 2021; Kovalchuk *et al.* 2020).

SYSTEMATIC PALAEONTOLOGY

Order Clupeiformes Bleeker, 1859
Suborder Clupeoidei Bleeker, 1859
Family indet.
Genus †*Beksinskiella* gen. nov.

DERIVATION OF NAME: Named after Zdzisław Beksiński, a Sanok-born Polish artist specializing in dystopian surrealism. He and his family greatly contributed over the years in many different aspects to the development of the Carpathian region in Poland.

TYPE SPECIES: †*Meletta longimana* Heckel, 1850.

DIAGNOSIS: Posterior part of the frontals ornamented with several striae; hypomaxilla absent; opercle smooth; 6 or 7 branchiostegal rays; vertebral column consisting of 42–48 vertebrae; 18–21 pectoral fin rays; 21–23 dorsal fin rays; preopercle smooth with arms similar in length; pelvic fins located near mid-length of dorsal fin base; 21–23 anal fin rays; two last anal fin rays elongated; caudal skeleton with two epurals; postpelvic scutes poorly developed; paddle-shaped urohyal with a rounded posterior margin.

REMARKS: †*Meletta longimana* (Heckel, 1850) was erected together with †*Meletta crenata* (Heckel, 1850) based on specimens from the Oligocene of Central Europe, and †*Meletta sardinites* (Heckel, 1850) based on specimens from the Miocene of Croatia. In the 20th century, the three species described by Heckel were synonymised and transferred to the genus *Clupea* Linnæus, 1758. †*Clupea longimana* and †*Clupea crenata* were placed in the synonymy of †*Clupea sardinites* (e.g., Jerzmańska 1960, 1968; Szymczyk 1978). Daniltshenko (1980) and Grande (1985) suggested the transfer of †*Clupea sardinites* to the genus *Sardinella* Valenciennes, 1847. Kovalchuk *et al.* (2020) reviewed clupeids from the Oligocene of the Central Paratethys. They referred specimens traditionally described as †*Sardinella sardinites* from the Polish Outer Carpathians, as well as specimens described by Heckel (1850) as †*Meletta longimana*, to a single species of †*Maicopiella* (Menner, 1949), i.e., †*M. longimana*.

The number of vertebrae in our specimens (44–48) is slightly greater than that reported by Kovalchuk *et al.* (2020), i.e., 42–45 (in *Maicopiella longimana*). The number of rays of the dorsal fin (17–19) given by Kovalchuk *et al.* (2020) is the number most frequently observed in our material but the best-preserved specimens show 21–23 rays. This is the result of poor preservation; the rays are very thin which makes their recognition difficult.

†*Beksinskiella longimana* (Heckel, 1850) comb. nov.
(Text-figs 2, 4–7)

1850. *Meletta longimana* n. sp.; Heckel, p. 231, pl. 25, figs. 1–3.
2020. *Maicopiella longimana* (Heckel, 1850); Kovalchuk *et al.*, fig. 5.

TYPE MATERIAL: The specimen depicted by Rzehak (1880, pl. 1, fig. 1), a skeleton with an incomplete skull (jaw bones not preserved), is hereby designated as the lectotype, as suggested by Kovalchuk *et al.* (2020). All other specimens described by Rzehak (1880) are recognised as paralectotypes.

REFERRED MATERIAL: 39 specimens (27 with counterparts, designated with ‘a–b’ in the collection numbers, see Appendix 1).

TYPE LOCALITY: Křepice (Krepitz), Czech Republic.

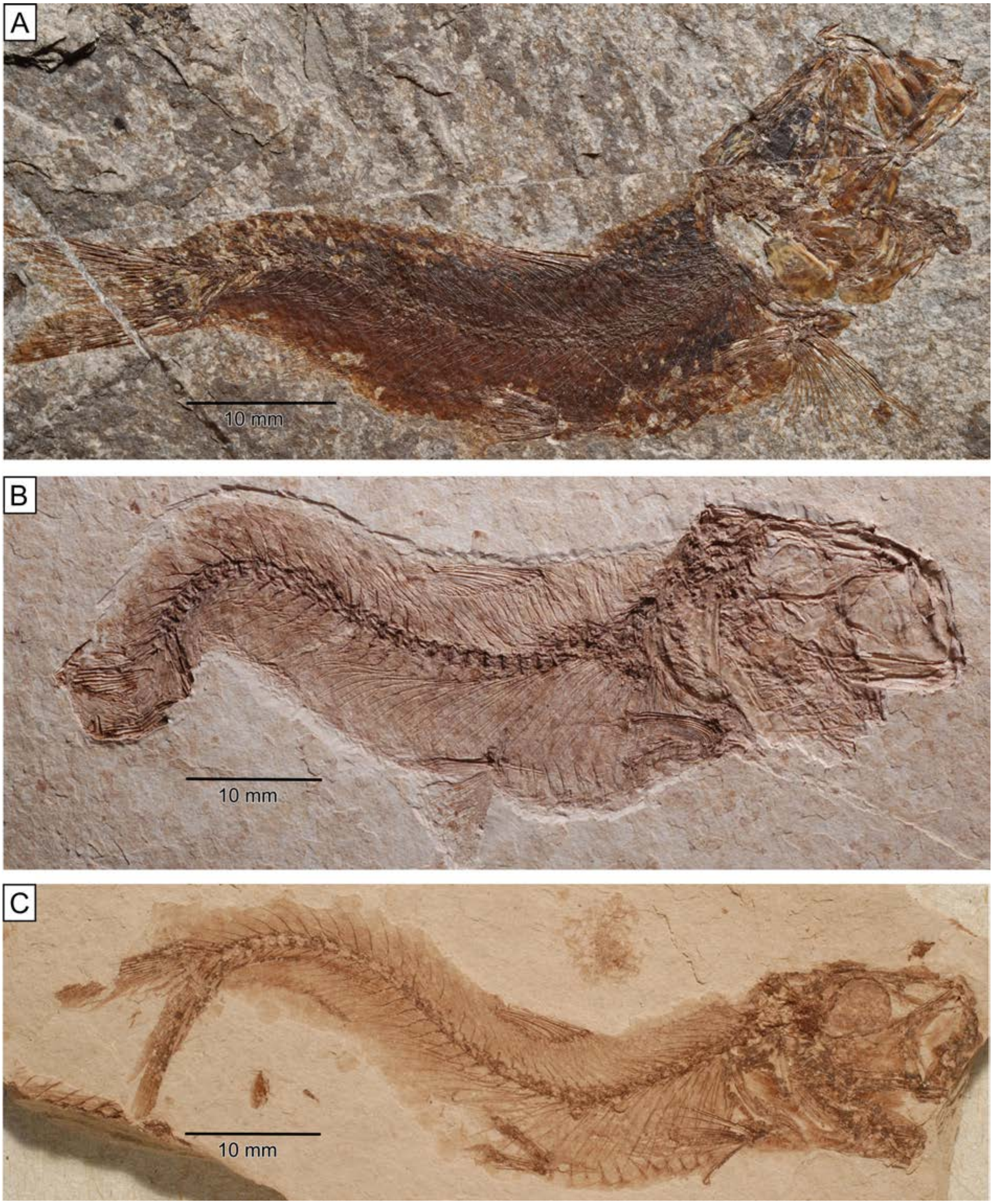
TYPE HORIZON: Lower Oligocene, Rupelian, NP 23 (see Brzobohatý and Bubík 2019 for details about the age of the fossiliferous deposits).

DIAGNOSIS: As for genus.

MEASUREMENTS: See Table 1.

DESCRIPTION: Small fishes with elongated and laterally compressed body, up to 90 mm of standard length (SL). The head is triangular in lateral view. Head length comprises 27–36% SL (Text-fig. 3). The mouth is small and terminal. The orbit is big and oval; the lower jaw articulation is located directly below (Text-fig. 4A, B). A complete series of abdominal keeled scutes is present with the pelvic scute being the largest. The postpelvic abdominal scutes are poorly developed.

Neurocranium. The neurocranium is elongated and triangular in lateral view. The paired frontals are the largest bones in the skull roof. They are triangular, pointed anteriorly, wider in the posterior part and narrow in the anterior part, which is slightly descending. In the posterior part they are ornamented



Text-fig. 2. †*Beksinskiella longimana* comb. nov. from the Oligocene of the Outer Carpathians, SE Poland. A – MWGUW ZI/57/119/a from Rudawka Rymanowska, B – MWGUW ZI/57/208/a from Futoma, C – MWGUW ZI/57/136/a from Jasienica Rosielna.

with several frontoparietal striae (Text-fig. 4C, D). The parasphenoid is long, thin, straight anteriorly, and slightly curved posteriorly. Most of the frontals are slightly dorsalo-ventrally compressed. The parietal, the supraoccipital and the epioccipital are sometimes partially visible posteriorly to the frontals and

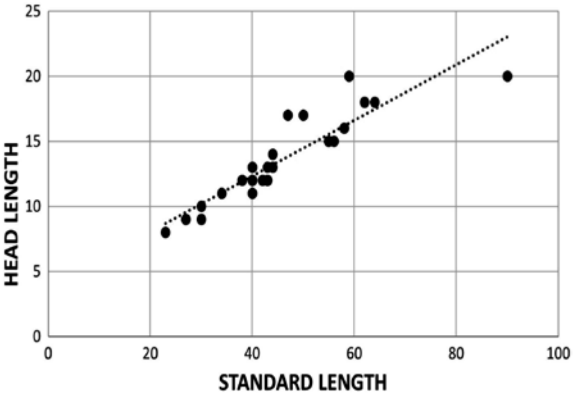
Morphometric character	MWGUW ZI/57/118	MWGUW ZI/57/119/a	MWGUW ZI/57/159	MWGUW ZI/57/161/1/b	MWGUW ZI/161/3/a	MWGUW ZI/57/168/b	MWGUW ZI/57/169	MWGUW ZI/57/173/1/b	MWGUW ZI/57/184/a	MWGUW ZI/57/185	Studied material
Standard length [SL]	38	56	47	30	27	59	42	64	90	23	23–90
Head length	12 (32)	15 (27)	17 (36)	9 (30)	9 (33)	20 (34)	12 (29)	18 (28)	–	8 (35)	8–20 (27–36)
Maximum body depth	6 (16)	12 (21)	11 (23)	8 (27)	6 (22)	10 (17)	7 (17)	12 (19)	19 (21)	5 (22)	5-19 (16–27)
Predorsal distance	18 (47)	23 (41)	26 (55)	14 (47)	11 (41)	30 (51)	20 (48)	28 (44)	43 (48)	12 (52)	11–43 (41–55)
Prepelvic distance	22 (58)	29 (52)	31 (66)	17 (57)	14 (52)	35 (59)	24 (57)	36 (56)	50 (56)	14 (61)	14–50 (52–66)
Preanal distance	31 (82)	41 (73)	39 (83)	24 (80)	–	48 (81)	36 (86)	49 (77)	–	18 (78)	18-49 (73–86)

Table 1. Morphometric characteristics of †*Beksinskiella longimana* comb. nov. Measurements are given in mm and as a percentage of the standard length (in parentheses). Number of specimens = 39.

the dorsal margin of the parietal articulates with the postero-ventral margin of the frontals. The pterotic and the sphenotic regions are not preserved in the studied material. The orbitosphenoid is a long bone that forms the orbit wall. The pterosphenoid connects dorsally with the frontals. The mesethmoid is a firm bone; it is anteriorly wider than its posterior part in lateral view. The lateral ethmoid articulates with the anterior part of the frontals; it is a small, subtriangular bone in lateral view.

Circumorbital series. The nasal appears to be small, but the margins of the bone are poorly preserved. The supraorbital extends from above the middle of the orbit to the anterior part of the frontals. The infraorbitals are poorly preserved. The first infraorbital lies ventral to the orbit and appears to be the largest bone of the series. The sclerotic ring is only partially preserved; its posterior part is not preserved but the anterior part extends in a crescent moon shape.

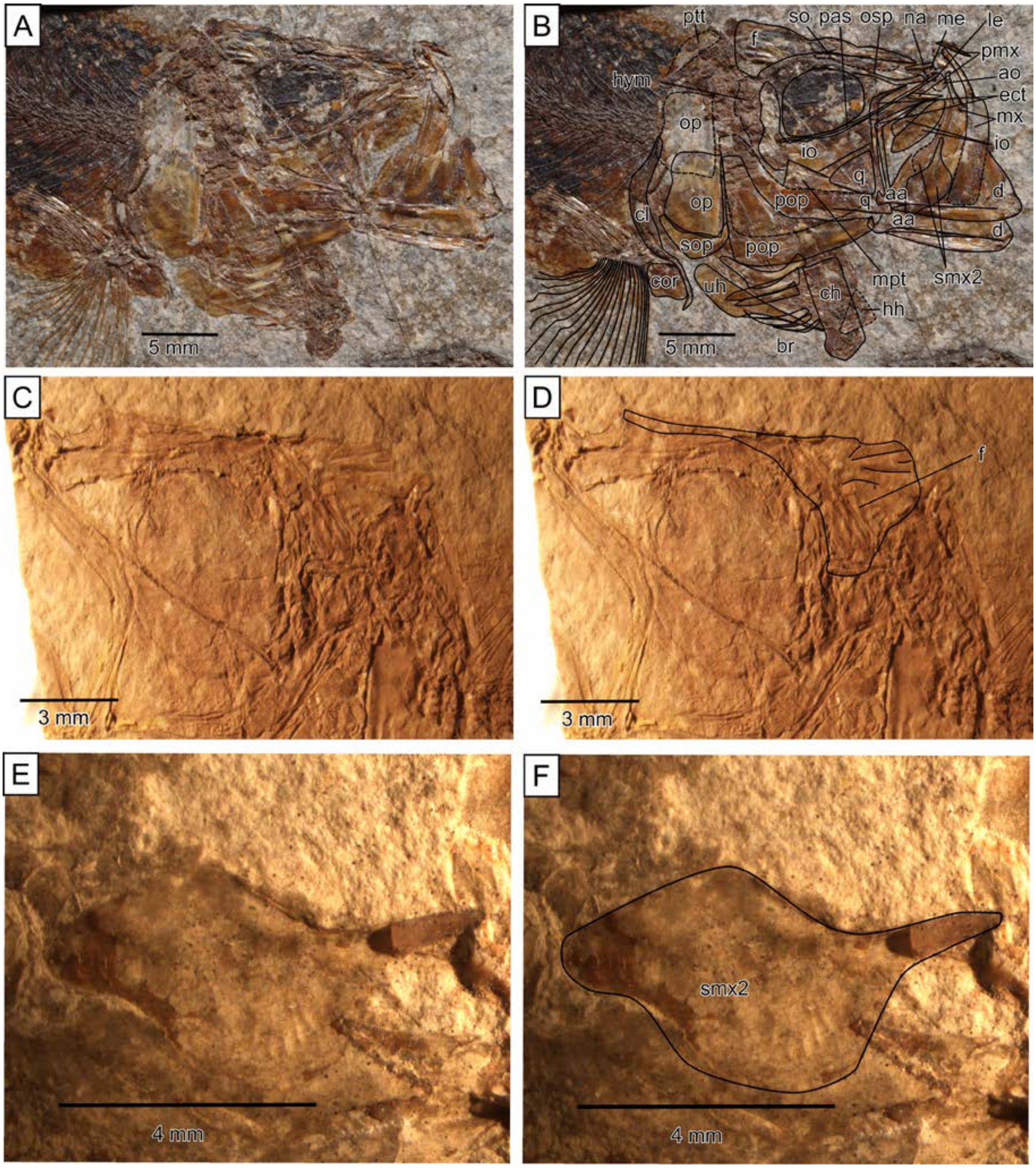
Jaws and dentition. The premaxilla is short, toothless, and curved in lateral view. The maxilla is narrow in the anterior part and wide in the posterior part. Its ventral margin is slightly convex, bearing small teeth in some of the specimens. There are two supramaxillae. The posterior supramaxilla has a narrow, slightly curved upwards anterior part, whereas the posterior part is robust. The posterior supramaxilla is asymmetrical. One weak ridge can be recognised from the anterior part of the bone to the central part where it fades away. The dorsal and ventral margins of the posterior part of the posterior supramaxilla are convex and rounded (Text-fig. 4E, F). The anterior supramaxilla is small and elongate. The hypomaxilla is absent. The outline of the mandible is a rounded trapezoidal with a straight ventral margin. The mandible is articulated with the skull beneath the anterior part of the orbit. The dentary is toothless and deep, together with the anguloarticular it appears subtriangular in shape. The ventral margin of the dentary is straight, its anteroventral angle is rounded. The anguloarticular has a poorly developed articular process.



Text-fig. 3. Cross-plot of head length *vs*. standard length of †*Beksinskiella longimana* comb. nov.

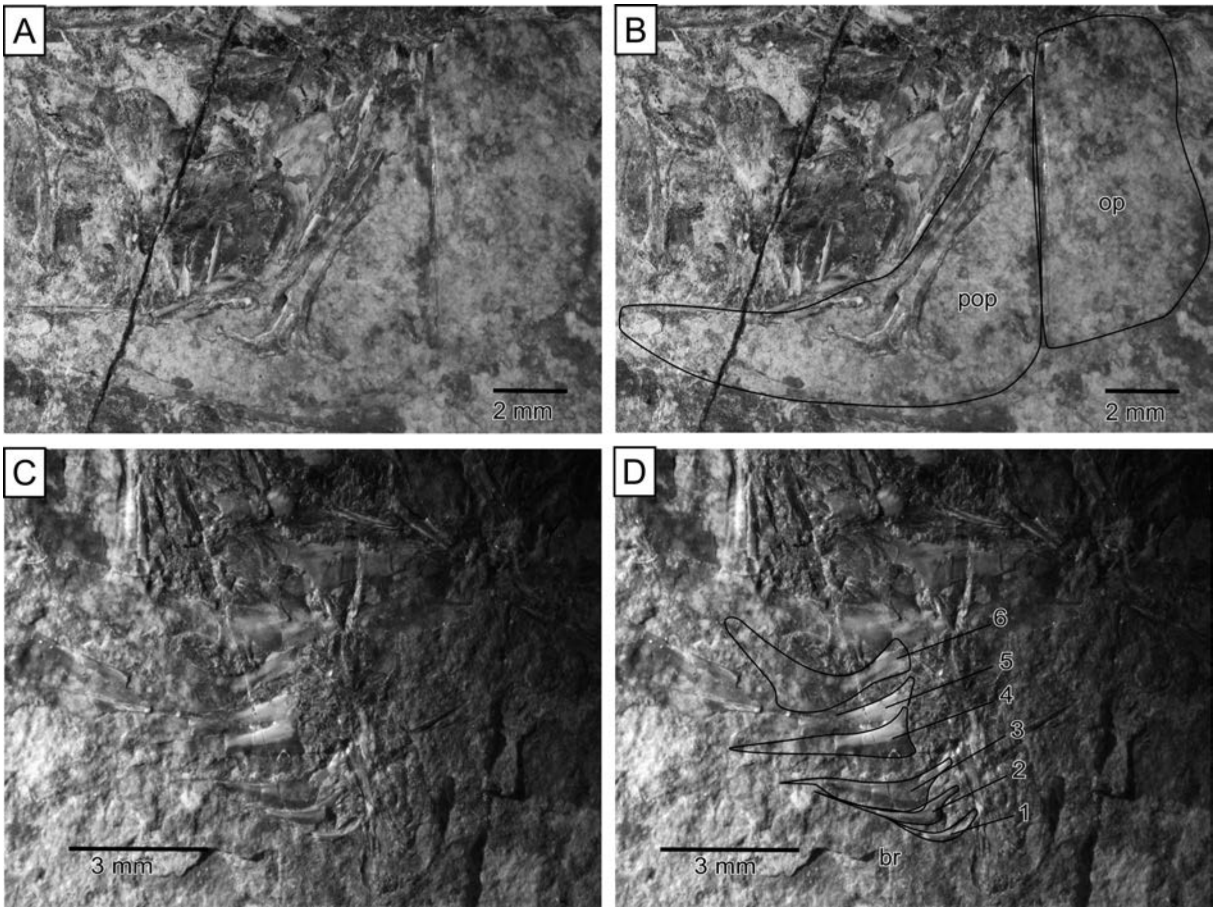
Suspensorium. The anterior margin of the palatine is thin and straight. The ectopterygoid is a thick, well-preserved bone; it forms an obtuse angle at its mid-length. The metapterygoid articulates anteriorly with the quadrate. The quadrate is triangular and the articulation with the mandible is located on the anteroventral margin. The symplectic is a thin bone firmly associated with the quadrate. The hyomandibula is poorly preserved in the studied material.

Opercular region. The preopercle is low with the ventral and dorsal arms similar in length. The arms form an obtuse angle. The surface of the preopercle is smooth except for the canal-bearing ridges in the middle of the bone between the arms. The opercle is smooth, high and wide (Text-fig. 5A, B). The posterior margin is convex and rounded with a small incision in the middle. The anterior margin is straight



Text-fig. 4. †*Beksinskiella longimana* comb. nov. from the Oligocene of the Outer Carpathians, SE Poland. A, B – Skull, MWGUW ZI/57/119/a from Rudawka Rymanowska; photo of specimen (A) and with superimposed interpretative drawing (B). C, D – Frontal, MWGUW ZI/57/088 from Jamna Dolna; photo of specimen (C) and with superimposed interpretative drawing (D). E, F – Second supramaxilla, MWGUW ZI/57/160/1/b from Rudawka Rymanowska; photo of specimen (E) and with superimposed interpretative drawing (F). Abbreviations: aa – anguloarticular; ao – antorbital; br – branchiostegal rays; ch – ceratohyal; cl – cleithrum; cor – coracoid; d – dentary; ect – ectopterygoid; f – frontal; hh – hypohyal; hym – hyomandibular; io – infraorbital; le – lateral ethmoid; me – mesethmoid; mtp – metapterygoid; mx – maxilla; na – nasal; op – opercle; osp – orbitosphenoid; pas – parasphenoid; pmx – premaxilla; pop – preopercle; ptt – posttemporal; q – quadrate; smx2 – second supramaxilla; so – supraorbital; sop – subopercle; uh – urohyal.

with its dorsal and ventral margins slightly rounded. On the opercle, near the anterior margin of the bone, occurs a vertically-oriented ridge. The ridge is distinctive and narrow in the dorsal part and slightly widens and weakens at the end of the ventral part. The subopercle envelopes the ventral margin of the



Text-fig. 5. A, B – Preopercle (pop) and opercle (op) of †*Beksinskiella longimana* comb. nov., MWGUW ZI/57/160/1/b from Rudawka Rymanowska; photo of specimen (A) and with superimposed interpretative drawing (B). C, D – Branchiostegal rays (1–6) to show the morphology of the last branchiostegal ray (6) of †*Beksinskiella longimana* comb. nov., MWGUW ZI/57/173/1 from Rudawka Rymanowska; photo of specimen (C) and with superimposed interpretative drawing (D).

opercle; its central part is wider than the anterior and posterior parts. The interopercle appears to be a long bone but its exact margins cannot be fully identified.

Hyoid and branchial arches. There are six or seven branchiostegal rays. The posterior rays are wide while the anterior rays are thin; rays in both parts appear to be long. The anterior edge of the last ray is rounded where the bone is attached to the hypohyal; its posterior part is a long, narrow lobe. The last branchiostegal ray is significantly curved at the dorsal edge and slightly curved at the ventral one. The anteroventral margin of this ray is positioned at an obtuse angle to the posteroventral one (Text-figs 4B, 5D). The urohyal is paddle-shaped; its anterior part is narrow and sharp, and widens towards the posterior part, the posterior part of the urohyal is high and rounded, its ventral margin is convex, and its dorsal margin is straight. In the middle of the bone there is a thin distinctive ridge parallel to the dorsal margin. The hyoid bar is poorly preserved in the studied material. The margin between posterior and anterior ceratohyal is not discernible; the anterior ceratohyal is slender in the middle of the bone in lateral view. The margin between the dorsal and ventral hypohyal is poorly preserved.

Vertebral column, ribs and intermuscular bones. The vertebral column consists of 44–48 vertebrae, including 15–18 caudal vertebrae. The three anterior abdominal vertebrae are covered by the opercle. The first preural centrum is triangular in lateral view. In the caudal region, neural spines are slightly curved and positioned approximately at 45º to the vertebrae centrum; haemal spines are positioned similarly. There are 25–28 pairs of ribs, which are thin, long and almost reaching the ventral body margin. At least three series of intermuscular bones are visible throughout the abdominal part of the vertebral column, two in the caudal region. The intermuscular bones are thin and delicate; one series is short and close to the vertebrae centra, clearly visible in the abdominal region, other series are longer covering haemal and neural spines. There are eight to ten supraneurals; they are thin and arched.

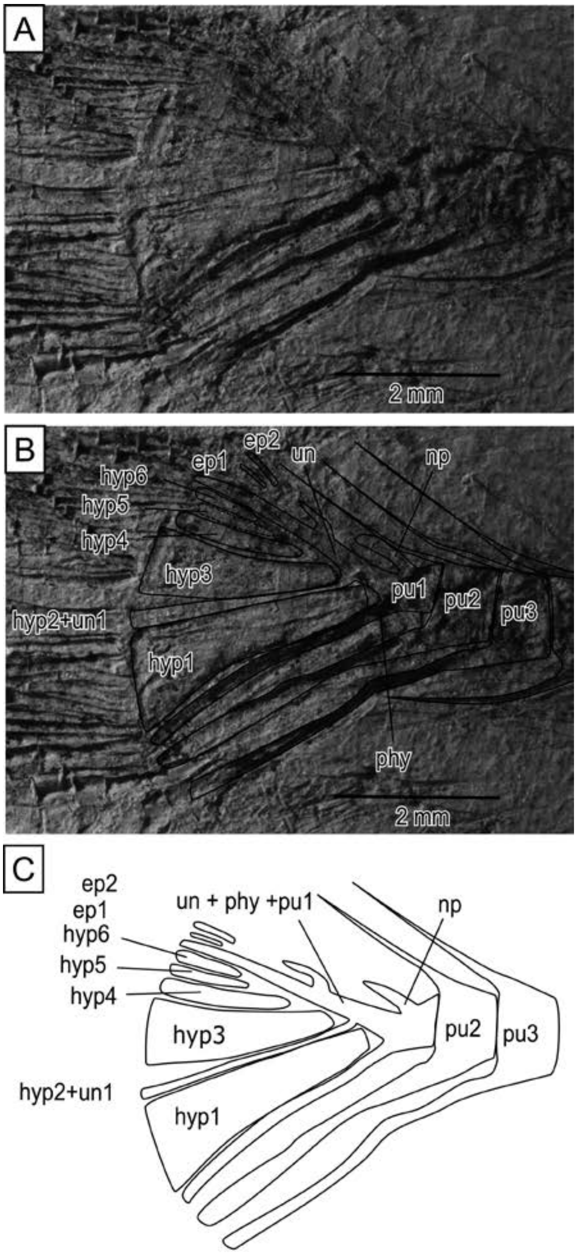
Dorsal fin. The dorsal fin is triangular and consists of 21–23 rays; the first anterior ray is shorter than the subsequent rays. There are 20–21 pterygiophores. The last pterygiophore is modified to a slender horizontally oriented stay. The dorsal fin is positioned in the middle of the body and originates above vertebrae 13th or 14th; it terminates above vertebrae 20th to 22nd.

Paired fins and girdles. The posttemporal is poorly preserved in the studied material. The pectoral fins are relatively long and consist of 18–21 rays. The first three rays are the longest. There are two rod-like postcleithra. The supracleithrum is long and curved posteriorly; the margin between supracleithrum and cleithrum can be traced near the vertebral column. The cleithrum is the longest bone in the pectoral gridle; it is S-shaped, covering the anterior margin of the coracoid. The coracoid is romboidal in lateral view. The pelvic fins are positioned beneath the middle of the dorsal fin and equal in length to vertebrae 4th to 5th. They originate below vertebrae 20th to 23rd. The pelvic bone is triangular in lateral view and equal in length to vertebrae 3rd to 4th, pointing anteriorly. The pelvic fin consists of 8–10 rays.

Anal fin. The anal fin consists of 21–23 rays and has 17–22 pterygiophores. It originates below vertebrae 30th to 35th and terminates below vertebrae 40th to 44th. Rays closer to the caudal fin are usually displaced. The anteriormost ray is shorter than the subsequent rays. The two last rays are elongated.

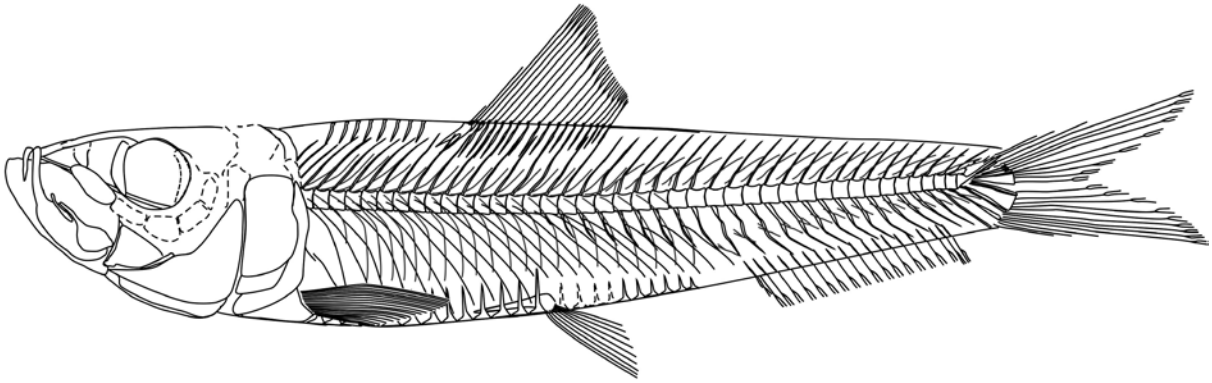
Caudal fin and skeleton. The caudal fin is forked and deeply notched. Six hypurals are present. Two epurals are visible. The second hypural is fused with the first ural centrum. The parhypural is long and firm but narrower than the first hypural (Text-fig. 6). The fin has nineteen principal caudal-fin rays (I, 9+8, I) and about fourteen procurrent rays.

Scales. All scales are cycloid with parallel grooves. These are the typical scales associated with clupeids. Isolated clupeid scales with a similar morphology appear in large numbers in the Oligocene rocks of the Outer Carpathians region (see Szymczyk 1978).



Text-fig. 6. A–C – Details of the caudal skeleton of †*Beksinskiella longimana* comb. nov., MWGUW ZI/57/030/b from Futoma; photo of specimen (A), with superimposed interpretative drawing (B), and reconstruction (C). Abbreviations: ep – epural; hyp – hypural; np – neural plate; phy – parhypural; pu – preural centrum; un – uroneural.

Abdominal scutes. The abdominal scutes form a continuous series between the isthmus and anal fin origin (Text-fig. 7). There are twelve to fourteen prepelvic scutes, each associated with the ventral portion of a pair of ribs; they are located posteriorly to the coracoid and end with the pelvic scute near the base of pelvic fins. There are at least eight postpelvic ones, which lie behind the pelvic scute but, due to their poor state of preservation, it is hard to point where exactly do they terminate. The postpelvic scutes are thin and smaller than the prepelvic



Text-fig. 7. Reconstruction of the skeleton of †*Beksinskiella longimana* comb. nov. from the Oligocene of the Outer Carpathians, SE Poland.

ones. All scutes bear ascending arms. The postpelvic scutes are poorly preserved and only a portion of the arms is visible.

DISCUSSION AND COMPARISONS

The following osteological and meristic data support the assignment of the examined specimens from the Oligocene of the Polish Outer Carpathians to a new genus, i.e., †*Beksinskiella* of the Suborder Clupeoidei (see Grande 1985): the presence of one or more abdominal scutes; the fusion of the second hypural with the first ural centrum; a separate first hypural; the fusion of the first uroneural with the first preural centrum; the size reduction of the first ural centrum, and the separation of the parhypural from the first ural centrum. The monophyletic status of five subfamilies currently recognised within the Family Clupeidae is under debate and not fully supported by morphological or molecular evidence (Grande 1985; Li and Ortí 2007; Lavoué *et al*. 2014; Wang *et al*. 2022). The presence of two long, rodlike postcleithra was a morphological character used by Grande (1985) as a diagnostic feature of the Clupeidae. Following the data of Wang *et al*. (2022), this feature is also present in species belonging to other clupeoid families.

†*Beksinskiella* gen. nov. (Text-fig. 7) differs from other members of the Suborder Clupeoidei in a unique combination of characters (see Table 2). The lack of the hypomaxilla bone distinguishes it from *Harengula* Valenciennes, 1847 and *Sardinella*. It differs from *Etrumeus* Bleeker, 1853, *Dussumieria* Valenciennes, 1847, *Spratelloides* Bleeker, 1851a and *Jenkinsia* Jordan and Evermann, 1896 in the absence of the peculiar, W-shaped, unkeeled pelvic scute. It lacks dorsal scutes which are present in †*Gosiutichthys* Grande, 1982, †*Knightia* Jordan, 1907, *Harengula*, and *Opisthonema* Gill, 1861. †*Beksinskiella* gen. nov. has 8–10 supraneurals, which distinguishes it from †*Chasmoclupea* Murray, Simons and Attia, 2005, †*Gosiutichthys*, †*Knightia*, †*Sarmatella* Menner, 1949, *Clupea*, *Clupeonella* Kessler, 1877, *Gilchristella* Fowler, 1935, *Opisthonema*, and *Sprattus* Girgensohn, 1846 (see Table 2). Poorly developed abdominal scutes, with 12–14 prepelvic ones distinguish it from †*Bolcaichthys* Marramà and Carnevale, 2015a, †*Chasmoclupea*, †*Gosiutichthys*, †*Karaganops* Baykina and Schwarzhans, 2017a, †*Maicopiella* (Menner, 1949), †*Primisardinella* Daniltshenko, 1968, †*Rupelia* Baykina and Kovalchuk, 2020 (Kovalchuk *et al*. 2020), *Amblygaster* Bleeker, 1849, *Gilchristella*, and *Sardinella* (see Table 2). †*Beksinskiella* gen. nov. differs from *Dussumieria*, †*Trollichthys* Marramà and Carnevale, 2015b, and †*Paretrumeus* Daniltshenko, 1980 in the presence of abdominal scutes. The new genus can be easily separated from †*Bolcaichthys*, †*Knightia*, *Clupea*, and *Opisthonema* by the presence of elongated two last rays of the anal fin. Sculptured frontals are a unique character that separate it from †*Maicopiella* and †*Sarmatella*. The combination of meristic data regarding numbers of rays in fins (dorsal fin 21–23, anal fin 21–23, pectoral fins 18–21, pelvic fins 8–10) is a distinguishing factor from †*Bolcaichthys*, †*Eoalosa* Marramà and Carnevale, 2018, †*Gosiutichthys*, †*Karaganops*, †*Knightia*, †*Maicopiella*, †*Pseudohilsa* Menner, 1949, †*Rupelia*, and †*Sarmatella* (see Table 2). The smooth opercle distinguishes it from *Alosa*, *Sardina* Antipa, 1904, *Sardinops* Hubbs, 1929, †*Moldavichthys* Baykina and Schwarzhans, 2017b, and †‘*Pomolobus*’. †*Beksinskiella* gen. nov. differs from *Clupea* in the number of branchiostegal rays (6–7). *Pellonula* Günther, 1868 differs from †*Beskinskiella* gen. nov. in having toothed premaxilla. *Rhinosardinia*

Taxon	Frontoparietal striae	Opercle	Branchiostegal rays	Supraneurals	Dorsal scutes	Hypomaxilla	Dorsal-fin pterygiophores	Anal-fin pterygiophores	Pectoral-fin rays	Pelvic-fin rays	Vertebrae	Abdominal scutes
Amblygaster	7–14	smooth	6	8	0	absent	18–20	17–18	16–19	8	43–44	0; 16–19; 11–15
Alosa	?	striations	7–8	9–13	0–1	?	12–20	15–23	?	9–11	46–57	?; ?
†*Beksinskiella* gen. nov.	4+	smooth	6–7	8–10	0	absent	19–20	17–22	18–21	8–10	44–48	0; 12–14; 8+
†*Bolcaichthys*	10–14	smooth	5–6	8	0	absent	15–16	15–16	14–18	8	40–42	0; 11–12; 10–11
†*Chasmoclupea*	?	smooth	?	13	0	absent	12	?	?	7	40+	4; 17; 5+
Clupea	?	smooth	8	15–19	0	absent	17–18	15–18	?	8–10	52–57	?; ?; ?
Clupeoides	?	smooth	2+	?	0	absent	11–17	15–26	?	7	?	7–12; 6–10
Clupeonella	?	smooth	7	11	0	absent	15	18–21	?	8	42	?; ?; ?
Dussumieria	?	?	12–17	21–22	?	?	19	14	?	8	55–56	?
†*Eoalosa*	?	?	?	13+	0	?	15	17	?	7	47	?
†*Eosardinella*	present	?	?	?	?	?	?	?	?	?	?	?
Etrumeus	?	?	11–16	10–12	?	?	19–20	9–11	?	8–9	49–56	?
Gilchristella	?	smooth	6–7	12–14	0	absent	15	19–21	?	7	40–41	0; 7–10; 0
†*Gosiutichthys*	?	smooth	7–8	6–7	12–13	absent	10–11	10–13	?	6–7	34–36	20–22
Harengula	3–5	smooth	6	7–10	1	present	16–17	14–19	?	8	40–42	?; ?; ?
Herklotsichthys	3–7	?	6	7–10	1	?	13–18	17–23	?	8	39–44	?
Jenkinsia	?	?	6–7	6–8	?	?	11–13	15	?	8	38–44	?
†*Karaganops*	present	smooth	7	10	0	absent	18–19	17–18	15	8–9	44–46	0; 13–15; 10
†*Knightia*	present	smooth	7–8	7–8	12–14	absent	11–14	13–17	11–14	7	37–39	?; ?; ?
†*Maicopiella*	absent	smooth	7	8–10	0	absent	19	17–18	17	8–9	42–45	0; 14–15; 10–11
†*Moldavichthys*	?	striations	7–8	9–10	0	?	16–17	17–18	?	8	39–44	?
Opisthonema	?	smooth	6	7–9	1	absent	18–19	18–22	?	8	45–47	?; ?; ?
†*Paretrumeus*	?	smooth	?	?	?	?	14–16	6–7	20–23	26–27	50–55	0; 0; 0
Pellonula	?	smooth	?	?	0	?	12–18	15–21	?	?	39–44	0–1+; 8–16; 6–11
†‘*Pomolobus*’		striations	?	?	0	?	14–17	17–22	14–18	8–9	40–43	?
†*Primisardinella*	?	smooth	?	9–10	0	absent	15–16	13–15	?	8	39–40	3–4; 10–11; 9–10
†*Pseudohilsa*	present	smooth	5?	10		absent	16	15–17	10+	7–9	40–42	3+; 11–12; 10–11
Rhinosardinia	?	?	5	10–12	0	?	13–15	14–16	?	8	36–43	?
†*Rupelia*	?	smooth	7	9	0	absent	20	16–18	19–20	9	48–50	0;15;10–11
Sardina	?	striations	7	10–11	0	absent	17–18	17–19	?	8	50–51	?; ?; ?
Sardinella	7–14	smooth	5–7	8–10	0	absent	16–19	16–20	13–18	8–9	43–48	0; 15–20; 11–16
Sardinops	?	striations	7–8	10	?	absent	18–19	17–18	?	8	50–52	?; ?; ?
†*Sarmatella*	?	smooth	7	10–12	0	absent	15–20	13–17	16–17	8–9	44–54	0; 22–24; 10–12
Spratelloides	?	?	7–8	9–11	?	?	10–14	10–14	?	7–8	41–50	?
Sprattus	?	smooth	7	15–17	0	absent	17–18	16–19	?	7–8	45–48	?; ?; ?
†*Trollichthys*	?	?	?	5–6	?	?	14–16	13	?	8	41–42	?

Table 2. Summary of selected morphological features used to discriminate the selected genera of the Suborder Clupeoidei. Abdominal scutes formula: scutes anterior to the coracoid; scutes between the coracoid and pelvic fin; scutes behind the pelvic fin. Prepelvic scutes comprise scutes anterior to the coracoid and scutes between the coracoid and pelvic fin. Comparative data was derived from Daniltshenko (1960, 1968, 1980), Grande (1982, 1985), Whitehead (1985), Murray *et al.* (2005), Baykina (2012, 2013a, b), Marramà and Carnevale (2015a, b, 2018), Baykina and Schwarzhans (2017a, b), Kevrekidis *et al.* (2021), and Kovalchuk *et al.* (2020).

Eigenmann, 1912 differs from †*Beskinskiella* gen. nov. by the presence of a sharp spine on the antero-posterior part of the maxilla.

Two additional unique osteologic characters that support our identification are related with the last branchiostegal ray and the urohyal. The last branchiostegal ray has a set of unique characters: a narrow and long posterior part of the bone, the anterior ventral edge being nearly straight, and the anterior edge rounded. Those features distinguish this bone from

Clupeonella, *Clupea*, *Sardina*, *Sardinops*, *Sprattus* and *Sardinella*, as well as †*Maicopiella*, †*Karaganops*, and †*Sarmatella*. The only genus that shows some significant similarities is †*Rupelia* from the Caucasus, which, however, differs in the presence of a groove in the central part of the last branchiostegal ray. The urohyal is slender, has a straight dorsal margin, and is low and sharp in the anterior part. The urohyal of *Sardinops* has a slenderer (in lateral view) and more curved shape, its dorsal margin is concave, and its posterior part is serrated (see Sato *et al.* 1988). The urohyal of †*Beskinskiella* gen. nov. differs also from that of *Harengula* and *Herklotsichthys* Whitley, 1951, which have a more oval shaped outline, and a rounded anterior part which is as high as the rest of the bone. The urohyal bone of †*Eosardinella* Sato, 1966 documented by Sato *et al.* (1988) show similarities with †*Beskinskiella* gen. nov. However, the differences include the curved posterior part of the bone and the higher anterior part of the bone in †*Eosardinella*. Differences are also found among the urohyal bones shown by Wongratana (1980) for the extant *Sardinella*. Even though the urohyals of different *Sardinella* species differ slightly in height, and in the ventral and dorsal margin outlines, most of them are higher than the urohyal of †*Beksinskiella* gen. nov. The urohyals of *Sardinella* species with a similar height as the urohyal of †*Beksinskiella* gen. nov. have a curved or concave dorsal margin. *Dussumieria* has a slenderer urohyal in lateral view and serration along the posterior margin. *Clupeoides* Bleeker, 1851b also shows a serration along the posterior part of the urohyal.

We found that there are small meristic and biometric differences between our specimens and those described by Kovalchuk *et al.* (2020) as †*Maicopiella longimana* from the Outer Carpathians of Poland. Small differences are in the body measurements, head length (27–36% SL *vs.* 26–34% SL) and predorsal length (41–55% SL *vs.* 43–51% SL) and higher number of vertebrae (44–48 *vs.* 42–45). The differences recognised in the body measurements seem to show a variability in the populations of the species. The higher number of vertebrae reflects the maximum number recognised in very well-preserved specimens. A smaller number of vertebrae was recognised in moderately well-preserved specimens due to the opercle covering a few vertebrae, so that either the limits between centra or some neural spines are not visible.

†*Beksinskiella longimana* comb. nov. is a new example of a clupeoid with an occurrence apparently restricted to the Paratethys; it is only known from the Oligocene of the Central Paratethys, from Poland, Ukraine and Czech Republic (Kovalchuk *et al.* 2020). Further research is necessary to verify the geographic distribution of this species. At present, †*B. longimana* comb. nov. is the second species with a well-documented osteology and recognised in the Oligocene Paratethys, the other being †*Rupelia rata* (Daniltschenko, 1959), described from the Oligocene of the Eastern Paratethys (Kovalchuk *et al.* 2020). Although clupeoids were abundant during the Oligocene in the Paratethys, many of the specimens have only been classified as Clupeidae indet. (Maxwell *et al.* 2016) or *Clupea* sp. (Kotlarczyk *et al.* 2006). Descriptions of other Oligocene clupeoid species by Daniltshenko (1960; †‘*Pomolobus*’ *antiquus*, †*P. curtus* and †*P. facilis*) and Ciobanu (1977; †*P. facilis*) are limited to meristic and biometric data, and some remarks on the osteology, and therefore cannot be adequately assessed.

Wang *et al.* (2022) present a new taxonomical classification within the Clupeiformes. Several subfamilies classified by Grande (1985) were upgraded to family level. The new proposal states that only a few genera classified by Grande (1985) to the Subfamily Clupeinae of the Clupeidae (*Clupea*; *Ramnogaster* Whitehead, 1965; *Sprattus*; *Strangomera* Whitehead, 1965) belong to the new Family Clupeidae making it monophyletic. Morphological characters were proposed to support the monophyly of some taxa, e.g., the Family Alosidae. The classification by Wang *et al.* (2022), like the classifications by Lavoué *et al.* (2014) and Grande (1985), lacks morphological characters diagnostic for each taxa. Following this classification, †*Beksinskiella* gen. nov. cannot be placed in any of the clupeoid families of Wang *et al.* (2022).

CONCLUSIONS

Osteological, morphometric and meristic analyses of clupeoid material from the Polish Outer Carpathians has revealed the presence of a new clupeoid genus, i.e., †*Beksinskiella*. This new genus, along with †*Rupelia* described by Kovalchuk *et al.* (2020), demonstrates a more diverse taxonomical composition of clupeoids in the Oligocene of the Paratethys than hitherto recognised. Our investigations further indicate that fossil species of the extant genera *Clupea* or *Sardinella* should not be expected to be found in the basin during that time. The presented anatomical description of †*B. longimana* comb. nov. provides a substantial improvement of our knowledge on the osteology of Oligocene clupeoids from the Central Paratethys. The new genus documents characteristic features in the branchiostegal rays, supramaxillae and urohyal. We believe that the results of our study will further contribute to improvement of the knowledge on the evolutionary history of clupeoids and palaeobiogeographic reconstructions in the Paratethys.

Acknowledgements

We would like to express our gratitude to Thomas Lunde Hygum, Wojciech Kozłowski, Rafał Nawrot, and the Spirifer Geological Society for collecting some of the specimens, and to Radosław Wasiluk for help during fieldwork. We acknowledge Giuseppe Marramà and Werner Schwarzhans for their valuable comments and reviews that significantly improved the quality of the manuscript. We would also like to thank an anonymous reviewer for comments on an earlier version of the manuscript.

REFERENCES

Antipa, G. 1904. Die Clupeinen des westlichen Teiles des Schwarzen Meeres und der Donaumündungen. *Anzeiger der Kaiserlichen Akademie der Wissenschaften*, *Mathematisch-Naturwissenschaftliche Classe*, **41** (19), 299–303.

Baykina, E.M. 2012. A new clupeid genus (Pisces, Clupeiformes, Clupeidae) from the Sarmatian of the Eastern Paratethys, Krasnodar Region. *Paleontological Journal*, **46**, 302–312.

Baykina, E.M. 2013a. A revision of *Clupea doljeana* Kramberger and *Sarmatella vukonovici* (Kramberger) (Pisces, Clupeidae) from the Sarmatian of Croatia. *Paleontological Journal*, **47**, 523–532.

Baykina, E.M. 2013b. Diagnostic importance of visceral skull bones of recent and fossil Clupeinae (Pisces, Clupeidae). *Journal of Ichthyology*, **53**, 687–701.

Baykina, E.M. and Schwarzhans, W.W. 2017a. Description of *Karaganops* n. gen. *perratus* (Daniltshenko 1970) with otoliths in situ, an endemic Karaganian (Middle Miocene) herring (Clupeidae) in the Eastern Paratethys. *Swiss Journal of Palaeontology*, **136** (1), 129–140.

Baykina, E.M. and Schwarzhans, W.W. 2017b. Review of "*Clupea humilis*" from the Sarmatian of Moldova and description of *Moldavichthys switshenskae* gen. et sp. nov. *Swiss Journal of Palaeontology*, **136** (1), 141–149.

Bieńkowska, M. 2004. Taphonomy of ichthyofauna from an Oligocene sequence (Tylawa Limestones horizon) of the Outer Carpathians, Poland. *Geological Quarterly*, **48**, 181–192.

Bieńkowska-Wasiluk, M. 2010. Taphonomy of Oligocene teleost fishes from the Outer Carpathians of Poland. *Acta Geologica Polonica*, **60**, 479–533.

Bieńkowska-Wasiluk, M. and Pałdyna, M. 2018. Taxonomic revision of the Oligocene percoid fish *Oligoserranoides budensis* (Heckel, 1856), from the Paratethys and paleobiogeographic comments. *Geologica Acta*, **16**, 75–92.

Bleeker, P. 1849. A contribution to the knowledge of the ichthyological fauna of Celebes. *Journal of the Indian Archipelago and Eastern Asia* (*Singapore*), **3** (1), 65–74.

Bleeker, P. 1851a. Nieuwe bijdrage tot de kennis der ichthyologische fauna van Celebes. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, **2**, 209–224.

Bleeker, P. 1851b. Nieuwe bijdrage tot de kennis der ichthyologische fauna van Borneo met beschrijving van eenige nieuwe soorten van zoetwatervisschen. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, **1** (3), 259–275.

Bleeker, P. 1853. Nalezingen op de ichthyologie van Japan. *Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen*, **25**, 1–56.

Bleeker, P. 1859. Enumeratio specierum piscium hucusque in Archipelago Indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. *Acta Societas Scientarum Indo-Neerlandaises*, **6**, 276.

Brzobohatý, R. and Bubík, M. 2019. Paleogene fish otoliths (Teleostei) from the Subsilesian and Ždánice units in Moravia. *Bulletin of Geosciences*, **94**, 101–114.

Ciobanu, M. 1977. The fossil fauna of the Piatra Neamt, 159 pp. Editura Academiei Republici Socialiste România; Bucuresti. [In Romanian]

Daniltshenko, P.G. 1960. Bony fishes of the Maikop Deposits of the Caucasus. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **78**, 1–208. [In Russian]

Daniltshenko, P.G. 1968. Upper Paleocene fishes of Turkmenia. In: Obrucev, D.V. (Ed.), Essays on the phylogeny and systematics of fossil fish and Agnatha, 113–156. Nauka; Moscow. [In Russian]

Daniltshenko, P.G. 1980. Order Clupeiformes. In: Novitskaya L.I. (Ed.), Bony fishes of the USSR. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **178**, 7–26. [In Russian]

Eigenmann, C.H. 1912. The freshwater fishes of British Guiana, including a study of the ecological grouping of species, and the relation of the fauna of the plateau to that of the lowlands. *Memoirs of the Carnegie Museum*, **5** (1), 1–578.

Figueiredo, F.J. 2009. A new marine clupeoid fish from the Lower Cretaceous of the Sergipe-Alagoas Basin, northeastern Brazil. *Zootaxa*, **2164**, 21–32.

Fowler, H.W. 1935. South African fishes received from Mr. H.W. Bell-Marley in 1935. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **87**, 361–408.

Gill, T.N. 1861. Synopsis of the subfamily of Clupeinae, with descriptions of new genera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **13**, 33–38.

Girgensohn, O.G.L. 1846. Anatomie und Physiologie des

Fisch-Nervensystems. *Mémoires de l'Académie Impériale des Sciences de Saint Pétersbourg*, **5**, 275–589.

Grande, L. 1982. A revision of the fossil genus †*Knightia*, with a description of a new genus from the Green River Formation (Teleostei, Clupeidae). *American Museum Novitates*, **2731**, 1–22.

Grande, L. 1985. Recent and fossil clupeomorph fishes with materials for revision of the subgroups of clupeoids. *Bulletin of the American Museum of Natural History*, **181**, 231–372.

Günther, A. 1868. Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Heteropygii, Cyprinidae, Gonorhynchidae, Hyodontidae, Osteoglossidae, Clupeidae, Chirocentride, Alepochephalide, Notopteride, Halosauridae, in the collection of the British Museum, 7, 1–512. Order of the Trustees; London.

Heckel, J.J. 1850. Beiträge zur Kenntniss der fossilen Fische Österreichs. *Denkschriften der Kaiserlischen Akademie der Wissenschaften Matematisch-Naturwissenschaftliche Classe*, **1**, 201–242.

Hubbs, C.L. 1929. The generic relationships and nomenclature of the California sardine. *Proceedings of the California Academy of Sciences* (Series 4), **18** (11), 261–265.

Jerzmańska, A. 1958. The state of research on the Tertiary fish in Poland. *Kwartalnik Geologiczny*, **12**, 177–186. [In Polish]

Jerzmańska, A. 1960. Ichthyofauna from the Jasło shales at Sobniów (Poland). *Acta Palaeontologica Polonica*, **5**, 367–419. [In Polish]

Jerzmańska, A. 1968. Ichtyofaune des couches à ménilite (Flysch des Karpathes). *Acta Palaeontologica Polonica*, **13**, 379–488.

Jerzmańska, A. 1979. Oligocene Alepocephaloid fishes from the Polish Carpathians. *Acta Palaeontologica Polonica*, **24**, 65–76.

Jordan, D.S. 1907. The fossil fishes of California; with supplementary notes on other species of extinct fishes. *Bulletin of the Department of Geology, University of California*, **5**, 95–145.

Jordan, D.S. and Evermann, B.W. 1896. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. *Bulletin of the United States National Museum*, **47**, 1–1240.

Kessler, K.F. 1877. The Aralo-Caspian Expedition. IV. Fishes of the Aralo-Caspio-Pontine ichthyological region, 360 pp. Stasulevicha; St. Petersburg.

Kevrekidis, C., Arratia, G., Bacharidis, N. and Reichenbacher, B. 2021. A new clupeid fish from the upper Miocene of Greece: A possible Hilsa relative from the Mediterranean. *Acta Palaeontologica Polonica*, **66**, 605–621.

Kotlarczyk, J. and Jerzmańska, A. 1988. Ichthyofauna in the stratigraphy of the Carpathians. *Przegląd Geologiczny*, **36** (6), 346–352. [In Polish]

Kotlarczyk, J., Jerzmańska, A., Świdnicka, E. and Wiszniowska, T. 2006. A framework of ichthyofaunal ecostratigraphy of the Oligocene–Early Miocene strata of the Polish Outer Carpathian basin. *Annales Societatis Geologorum Poloniae*, **76**, 1–111.

Kovalchuk, O., Baykina, E., Świdnicka, E., Stefaniak, K. and Nadachowski, A. 2020. A systematic revision of herrings (Teleostei, Clupeidae, Clupeinae) from the Oligocene and early Miocene from the eastern Paratethys and the Carpathian Basin. *Journal of Vertebrate Paleontology*, **40** (2), e1778710.

Lavoué, S., Konstantinidis, P. and Chen, W. 2014. Progress in Clupeiform systematics. In: Ganias, K. (Ed.), Biology and ecology of sardines and anchovies, 3–42. CRC Press; Boca Raton.

Lavoué, S., Miya, M., Musikasinthorn, P., Chen, W.J. and Nishida, M. 2013. Mitogenomic evidence for an Indo-West Pacific origin of the Clupeoidei (Teleostei: Clupeiformes). *PloS ONE*, **8**, e56485.

Li, C. and Ortí, G. 2007. Molecular phylogeny of Clupeiformes (Actinopterygii) inferred from nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **44**, 386–398.

Linck, H.F. 1790. Versuch einer Eintheilung der Fische nach den Zähnen. *Magazin für das Neueste aus der Physik und Naturgeschichte*, **6** (3), 28–38.

Linnæus, C. 1758. Systema Naturae. 10th edition, 824 pp. Laurentii Salvii; Stockholm.

Marramà, G. and Carnevale, G. 2015a. The Eocene sardine †*Bolcaichthys catopygopterus* (Woodward, 1901) from Monte Bolca, Italy: osteology, taxonomy, and paleobiology. *Journal of Vertebrate Paleontology*, **35**, e1014490.

Marramà, G. and Carnevale, G. 2015b. Eocene round herring from Monte Bolca, Italy. *Acta Palaeontologica Polonica*, **60**, 701–710.

Marramà, G. and Carnevale, G. 2018. *Eoalosa janvieri* gen. et sp. nov., a new clupeid fish (Teleostei, Clupeiformes) from the Eocene of Monte Bolca, Italy. *Paläontologische Zeitschrift*, **92**, 107–120.

Maxwell, E.E., Alexander, S., Bechly, G., Eck, K., Frey, E., Grimm, K., Kovar-Eder, J., Mayr, G., Micklich, N., Rasser, M., Roth-Nebelsick, A., Salvador, R.B., Schoch, R.R., Schweigert, G., Stinnesbeck, W., Wolf-Schwenninger, K. and Ziegler, R. 2016. The Rauenberg fossil Lagerstätte (Baden-Württemberg, Germany): a window into early Oligocene marine and coastal ecosystems of Central Europe. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **463**, 238–260.

Menner, V.V. 1949. Class Pisces. In: Zabelin, A.G. (Ed.), Atlas of index forms of fossil faunas of the USSR, 13, 346–360. Gosgeolitizdat; Moscow. [In Russian]

Murray, A.M., Simons, E.L. and Attia, Y.S. 2005. A new clupeid fish (Clupeomorpha) from the Oligocene of Fayum, Egypt, with notes on some other fossil clupeomorphs. *Journal of Vertebrate Paleontology*, **25**, 300–308.

Nelson, J.S., Grande, T.C. and Wilson, M.V.H. 2016. Fishes of the World, fifth edition, 707 pp. John Wiley and Sons, Inc.; Hoboken, New Jersey.

Pharisat, A. and Micklich, N. 1998. Oligocene fishes in the western Paratethys of the Rhine Valley Rift System*. Italian Journal of Zoology* (Suppl.), **65** (S1), 163–168.

Popov, S.V., Akhmetiev, M.A., Bugrova, E.M., Lopatin, A.V., Amitrov, O. V., Andreyeva-Grigorovich, A., Zaporozhets, N.I., Zherikhin, V.V., Krasheninnikov, V.A., Nikolaeva, I.A., Sytchevskaya, E.K. and Shcherba, I.G. 2002. Biogeography of the Northern Peri-Tethys from the Late Eocene to the Early Miocene: Part 2. Early Oligocene. *Paleontological Journal*, **36** (Suppl. 3), 185–259.

Přikryl, T., Kania, I. and Krzemiński, W. 2016. Synopsis of fossil fish fauna from the Hermanowa locality (Rupelian; Central Paratethys; Poland): current state of knowledge. *Swiss Journal of Geosciences*, **109**, 429–443.

Rafinesque, C.S. 1820. Ichthyologia Ohiensis. *Review and Miscellaneous Western Magazine*, **2** (3), 169–177.

Rzehak, A. 1880. Ueber das Vorkommen und die geologische Bedeutung der Clupeidengattung Meletta Valenc. in den österreichischen Tertiärschichten. *Verhandlungen des naturforschenden Vereins in Brünn*, **19**, 61–82.

Sato, Y. 1966. A new genus and species of sardine from the Miocene Hishinai Formation, northeastern Japan. *Japanese Journal of Ichthyology*, **13**, 112–125.

Sato, Y., Hasegawa, Y. and Yonezawa, A. 1988. The urohyal of Japanese Miocene Clupeid Fish *Eosardinella hishinaiensis*. *Science Reports of the Yokohama National University, Section II*, **35**, 57–59.

Smirnov, V.P. 1936. Fishes of the North Caucasian Oligocene (Chernorechensk Region). *Trudy Uzbekskogo Gosudarstvennogo Universiteta*, **5**, 1–92. [In Russian]

Svetovidov, A.N. 1952. Fauna of the USSR. Fishes. Vol. 2, is. 1. Clupeidae, 331 pp. Academy of Sciences of the USSR; Moscow-Leningrad. [In Russian]

Szymczyk, W. 1978. Clupeid scales from the Menilite Beds (Palaeogene) of the Carpathians. *Acta Palaeontologica Polonica*, **23**, 387–407.

Valenciennes, A. 1847. De la famille des Clupéoïdes. In: Cuvier, G. and Valenciennes, A. (Eds), Histoire naturelle des poissons. Livre vingt et unième, vol. 20, 472 pp. P. Bertand; Paris.

Wang, Q., Dizaj, L.P., Huang, J., Sarker, K.K., Kevrekidis, C., Reichenbacher, B., Esmaeili, H.R., Straube, N., Moritz, T. and Li, C. 2022. Molecular phylogenetics of the Clupeiformes based on exon-capture data and a new classification of the order. *Molecular Phylogenetics and Evolution*, **175**, 107590.

Wasiluk, R. 2013. Karta Dokumentacyjna Geostanowiska (Numer KDG: 4852) Kamieniołom łupków menilitowych w Jasienicy Rosielnej. [available at: http://geostanowiska.pgi.gov.pl/gsapp_v2/ObjectDetails.aspx?id=4852] [Last accessed: 12.2022]

Whitehead, P.J.P. 1965. A new genus and subgenus of clupeid fishes and notes on the genera *Clupea*, *Sprattus* and *Clupeonella*. *Annals and Magazine of Natural History* (Series 13), **7** (78) (for 1964), 321–330.

Whitehead, P.J.P. 1985. Clupeoid fishes of the World. An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part I – Chirocentridae, Clupeidae and Pristigasteridae. *FAO Fisheries Synopsis*, **125** (7/1), 1–303.

Whitehead, P.J.P. and Teugels, G. 1985. The West African pygmy herring *Sierrathrissa leonensis*: general features, visceral anatomy, and osteology. *American Museum Novitates*, **2835**, 1–44.

Whitley, G.P. 1951. New fish names and records. *Proceedings of the Royal Zoological Society of New South Wales*, **70** (for 1949–50), 61–68.

Wongratana, T. 1980. Systematics of Clupeoid Fishes of the Indo-Pacific Region. Unpublished PhD thesis, 432 pp. University of London; London.

Manuscript submitted: 16th August 2023
Revised version accepted: 15th January 2024

APPENDIX 1

List of specimens of †*Beksinskiella longimana* comb. nov. with their localities.

Specimen	Locality
MWGUW ZI/57/030/b	Futoma
MWGUW ZI/57/082/1/b	Rudawka Rymanowska
MWGUW ZI/57/087	Dobra Góra
MWGUW ZI/57/088	Jamna Dolna
MWGUW ZI/57/117/a–b	Jasienica Rosielna
MWGUW ZI/57/118	Jasienica Rosielna
MWGUW ZI/57/119/a–b	Rudawka Rymanowska
MWGUW ZI/57/136/a–b	Jasienica Rosielna
MWGUW ZI/57/159/a–b	Futoma
MWGUW ZI/57/160/1/a–b	Rudawka Rymanowska
MWGUW ZI/57/161/1/a–b	Rudawka Rymanowska
MWGUW ZI/57/161/2/a–b	Rudawka Rymanowska
MWGUW ZI/57/161/3/a–b	Rudawka Rymanowska
MWGUW ZI/57/162/a–b	Rudawka Rymanowska
MWGUW ZI/57/163	Futoma
MWGUW ZI/57/164/a–b	Jasienica Rosielna
MWGUW ZI/57/165/a–b	Jasienica Rosielna
MWGUW ZI/57/166/1	Jasienica Rosielna
MWGUW ZI/57/167	Jasienica Rosielna
MWGUW ZI/57/168/a–b	Jasienica Rosielna
MWGUW ZI/57/169/a–b	Jasienica Rosielna
MWGUW ZI/57/170/a–b	Jasienica Rosielna
MWGUW ZI/57/172/a–b	Hermanowa
MWGUW ZI/57/173/1/a–b	Rudawka Rymanowska
MWGUW ZI/57/173/2/a–b	Rudawka Rymanowska
MWGUW ZI/57/174/a–b	Rudawka Rymanowska
MWGUW ZI/57/175	Rudawka Rymanowska
MWGUW ZI/57/176/a–b	Rudawka Rymanowska
MWGUW ZI/57/180/a–b	Rudawka Rymanowska
MWGUW ZI/57/183	Jasienica Rosielna
MWGUW ZI/57/184/a–b	Jasienica Rosielna
MWGUW ZI/57/185/a–b	Futoma
MWGUW ZI/57/186	Futoma
MWGUW ZI/57/187/a–b	Rudawka Rymanowska
MWGUW ZI/57/207/a–b	Hermanowa
MWGUW ZI/57/208/a–b	Futoma
MWGUW ZI/57/209	Jasienica Rosielna
MWGUW ZI/57/210/a–b	Jamna Dolna
MWGUW ZI/57/211/a–b	Jamna Dolna