www.czasopisma.pan.pl PAN www.journals.pan.pl

Acta Geologica Polonica, Vol. 74 (2024), No. 3, e23
DOI: 10.24425/agp.2024.151753

A new extinct shad from Poland in the light of clupeiform diversity and distribution within the Paratethys during the Oligocene

MALGORZATA BIENKOWSKA-WASILUK[1], MATEUSZ GRANICA[1] and OLEKSANDR KOVALCHUK[2,3]

[1] *University of Warsaw, Faculty of Geology, Żwirki i Wigury 93, 02-089 Warszawa, Poland; e-mails: m.wasiluk@uw.edu.pl; m.granica2@uw.edu.pl*
[2] *University of Wrocław, Faculty of Biological Sciences, Department of Palaeozoology, Sienkiewicza 21, 50-335 Wrocław, Poland;*
[3] *National Museum of Natural History of the National Academy of Sciences of Ukraine, Department of Palaeontology, Bohdana Khmelnytskoho 15, 01054 Kyiv, Ukraine; e-mail: biologiest@ukr.net*

ABSTRACT:

Bienkowska-Wasiluk, M., Granica M. and Kovalchuk, O. 2024. A new extinct shad from Poland in the light of clupeiform diversity and distribution within the Paratethys during the Oligocene. *Acta Geologica Polonica*, **74** (3), e23.

The Order Clupeiformes Bleeker, 1859 comprises herrings, anchovies, sprats, sardines, and shads. The fossil record of this group is rich within the Paratethys. Here we describe a new clupeiform fish, †*Sanalosa janulosa* gen. et sp. nov., from the Lower Oligocene of the Carpathian Basin, Poland. This new genus has a unique combination of characters (lower jaw articulation located under the posterior part of the orbit; abdominal scutes well developed with 3 to 5 in the gular region, 11–14 prepelvic scutes associated with ribs, 11–12 postpelvic scutes; several striae on the frontals; an opercle with 6–12 thin radial ridges; a horizontal ramus of the preopercle shorter than the vertical one; 42–44 vertebrae; 8–10 supraneurals; a dorsal fin with 18–22 rays, and an anal fin with 21–23 rays), supporting recognition of a new genus and species within the Family Alosidae Svetovidov, 1952. Similarities and differences between fossil and extant genera of the Clupeiformes are discussed to shed more light on their relationship. Moreover, the palaeobiogeography, diversity and distribution of Oligocene clupeiform fishes in the Paratethys are presented and discussed.

Key words: Teleostei; Alosidae; New genus; Paratethys; Oligocene; Menilite Formation.

https://zoobank.org/References/db413df2-7645-4deb-a1ab-9b74378493fa

INTRODUCTION

The large and taxonomically diverse Order Clupeiformes Bleeker, 1859 includes more than 400 extant species of herrings, anchovies, sprats, sardines, shads, and menhadens (Fricke *et al.* 2024). Representatives of this group have a wide (mostly tropical) distribution, and they are one of the most intensely commercially exploited fishes worldwide (FAO 2022). Clupeiforms are primarily marine, although some of them are freshwater and anadromous (Nelson *et al.* 2016). They are medium-sized fishes, usually in the 150–250 mm length range (e.g., Whitehead 1985). Most clupeiform species form schools and swim near the surface, usually in coastal waters, feeding on plankton (Whitehead 1985; Nelson *et al.* 2016).

There is no consensus regarding the classification of the Clupeiformes, although the classification of

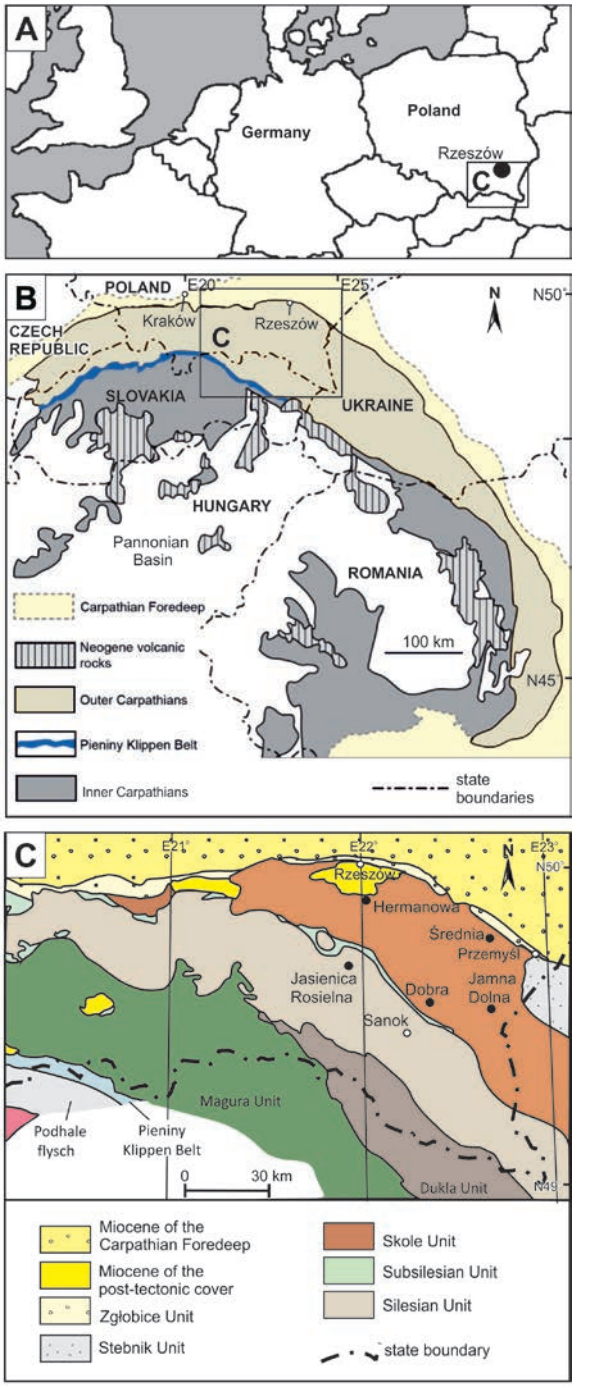
Wang *et al.* (2022) used herein seems to fill a significant gap in taxonomic issues albeit some taxa of this group are not defined by morphological characters.

Although the fossil skeletal record of the Clupeiformes is rich (e.g., Daniltshenko 1960, 1980; Grande 1985; Murray *et al.* 2005; Baykina 2012, 2013a, b; Marramà and Carnevale 2015a, b, 2018; Baykina and Schwarzhans 2017a, b; Kovalchuk *et al.* 2020; Granica *et al.* 2024), our knowledge on extinct representatives is still insufficient, and their evolutionary history and past diversity remain ambiguous and poorly understood. The commonly used classification of clupeiform fossils by Grande (1985) differs significantly from that proposed by Wang *et al.* (2022), for example in the understanding of the scope of the Family Clupeidae Cuvier, 1817. It is a large and diverse family in Grande (1985), but reduced to seven genera in Wang *et al.* (2022), including only four genera of the Subfamily Clupeinae Cuvier, 1817 *sensu* Grande (1985) and three others representing the subfamilies Alosinae Svetovidov, 1952 *sensu* Grande (1985) and Pellonulinae Whitehead, 1985. Wang *et al.* (2022) recognised the Family Alosidae Svetovidov, 1952 with four genera: *Alosa* Linck, 1790; *Brevoortia* Gill, 1861; *Sardina* Antipa, 1904; and *Sardinops* Hubbs, 1929, but without any subfamilies. The genera *Alosa* and *Brevoortia* were classified by Grande (1985) to the Alosinae, while the genera *Sardina* and *Sardinops* – to the Clupeinae. Understanding the interrelationships of fossil taxa in the light of current taxonomy is challenging and needs a thorough revision.

The Oligocene deposits of the Menilite Formation from the Outer Carpathians of Poland hold a unique fossil fish record including extremely numerous remains of clupeiforms usually represented by complete or fragmented skeletons and isolated scales. In this study, a new clupeiform fish is described from the Oligocene deposits of Poland. The diversity and palaeobiogeography of the Clupeiformes during the Oligocene are discussed. Our investigation sheds new light on the evolution, distribution, and diversity of this group in the Paratethys.

LOCALITIES AND THEIR STRATIGRAPHIC POSITION

The specimens were collected from five localities situated in the Podkarpackie Voivodeship, southern Poland, from the Oligocene deposits of the Silesian and Skole units or nappes of the Outer Carpathians (Text-fig. 1). Four localities (Dobra Góra, Hermanowa, Jamna Dolna, and Średnia) expose the Skole Unit,



Text-fig. 1. Location maps. A – Study area within Central Europe; B – Study area within simplified geological map of the Outer Carpathians (modified from Kováč *et al.* 1998); C – Localities where the specimens were collected (black dots) within simplified geological map of the Polish part of the Outer Carpathians (modified from Żytko *et al.* 1989).

whereas a single locality (Jasienica Rosielna) lies within the Silesian Unit.

The Dobra Góra locality (DG in Kotlarczyk *et*

al. 2006) lies 15 km north-east of Sanok city. The Hermanowa locality (HE in Kotlarczyk *et al.* 2006; Přikryl *et al.* 2016) is located 10 km south of Rzeszów city. The Jamna Dolna locality (JD1 in Kotlarczyk *et al.* 2006; Bienkowska-Wasiluk 2010) is 20 km south-west of Przemyśl city. Średnia (SR in in Kotlarczyk *et al.* 2006) is 15 km west of Przemyśl city. In these four localities, the specimens were obtained from the Rudawka Tractionite Member Unit, ichthyofaunal zone IPM 2. The Jasienica Rosielna locality (Wasiluk 2013) is 30 km south of Rzeszów city. In this locality the specimens come from the upper part of the Menilite Formation, ichthyofaunal zone IMP2. The ichthyofaunal zone IPM2 is correlated with the calcareous nannoplankton Biozone NP23 (Kotlarczyk *et al.* 2006).

MATERIAL AND METHODS

The material used in this study is housed in the Museum of the Faculty of Geology, University of Warsaw (MWGUW, Muzeum Geologiczne im. Stanisława Józefa Thugutta) and in the Department of Palaeozoology, University of Wrocław, Wrocław (ZPALWr.), Poland. It consists of six complete and almost complete articulated skeletons in the MWGUW collection and one complete skeleton in the ZPALWr. collection. The specimens were studied under a stereomicroscope NIKON SMZ1000 at the Scanning Electron and Optical Microscopy Laboratory at the Faculty of Geology of the University of Warsaw. All fishes were measured as standard length (SL), which is the length of a specimen measured from the anterior tip of the snout to the posterior margin of the hypurals. The osteological terminology follows Grande (1985), and Whitehead and Teugels (1985). All extinct taxa are marked with a dagger (†) preceding their name. Comparative information about the Clupeiformes was mostly derived from Daniltshenko (1960, 1980), Grande (1985), Whitehead (1985), Murray *et al.* (2005), Baykina (2012, 2013a, b, 2015), Marramà and Carnevale (2015a, b, 2018), Baykina and Schwarzhans (2017a, b), Kovalchuk *et al.* (2020), Kevrekidis *et al.* (2021), Fricke *et al.* (2024), Froese and Pauly (2024), and Granica *et al.* (2024).

Table 1. Specimens of †*Sanalosa janulosa* gen. et sp. nov. and localities from which they were obtained.

Number of specimen	Type of material	Locality
MWGUW ZI/57/215/a-b	holotype	Jamna Dolna
MWGUW ZI/57/182	paratype	Dobra Gora
MWGUW ZI/57/171/1/a-b	paratype	Hermanowa
MWGUW ZI/57/214/a-b	paratype	Jasienica Rosielna
MWGUW ZI/57/133	material	Jasienica Rosielna
MWGUW ZI/57/219	material	Podkarpackie Voivodeship
ZPALWr. N/6407	material	Srednia

SYSTEMATIC PALAEONTOLOGY

Subdivision Teleostei Müller, 1846 *sensu* Arratia, 1999
Order Clupeiformes Bleeker, 1859 *sensu* Wang, Dizaj, Huang, Sarker, Kevrekidis, Reichenbacher, Esmaeili, Straube, Moritz and Li, 2022
Suborder Clupeoidei Bleeker, 1859
Family Alosidae Svetovidov, 1952

Genus †*Sanalosa*, gen. nov.

TYPE SPECIES: †*Sanalosa janulosa* sp. nov.

DIAGNOSIS: Lower jaw articulation located under the posterior part of the orbit; abdominal scutes well developed (including 3 to 5 scutes in the gular region, 11–14 prepelvic, associated with ribs, and 11–12 postpelvic scutes); several striae on the frontals; opercle with 6–12 thin radial ridges; horizontal ramus of the preopercle shorter than the vertical one; 42–44 vertebrae; 8 to 10 supraneurals; dorsal fin with 18–22 rays, and anal fin with 21–23 rays.

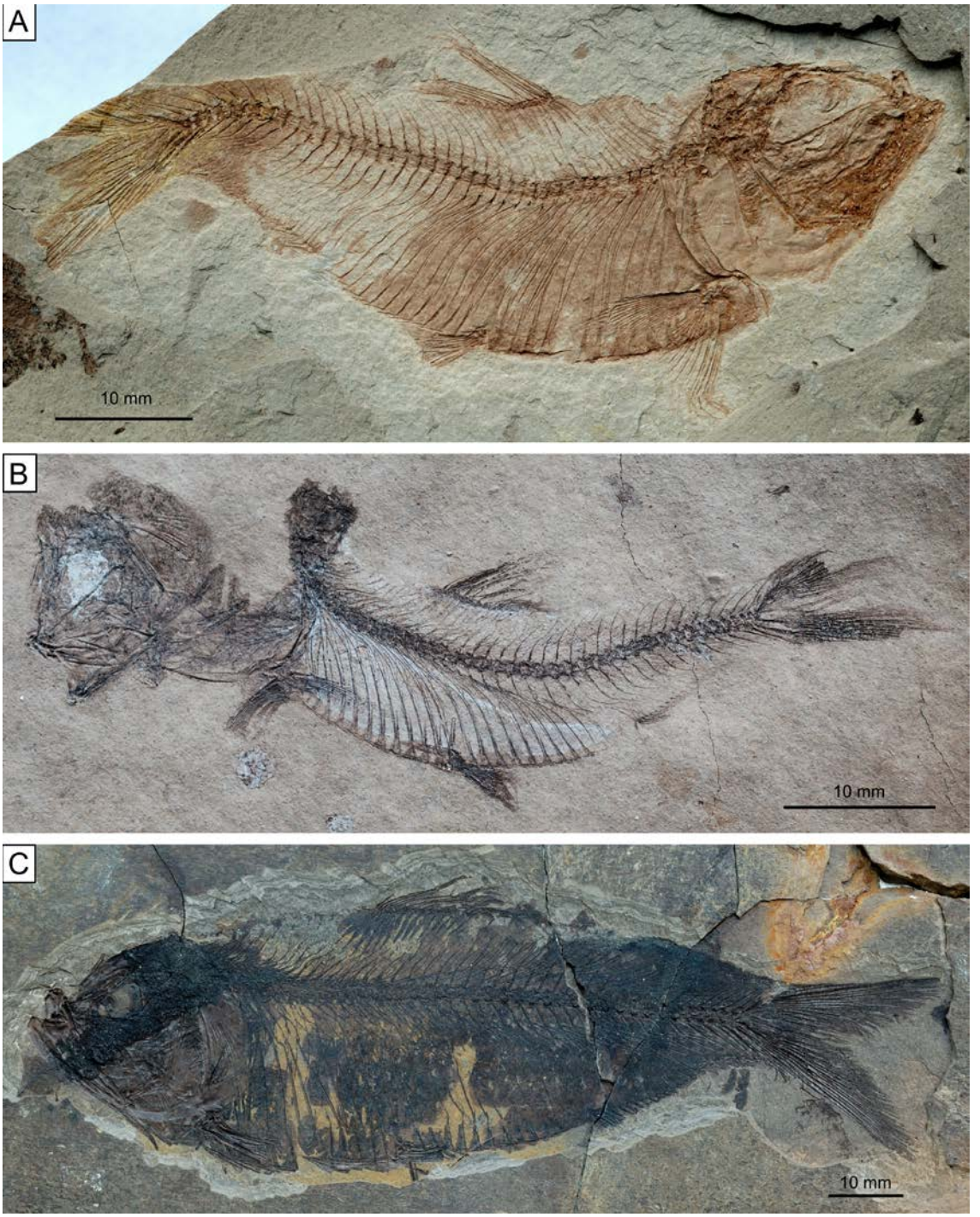
DERIVATION OF NAME: In reference to the San River (close to which the fossils considered were found) added to the Latin word *Alosa* meaning ‘shad’.

†*Sanalosa janulosa* gen. et sp. nov.
(Text-figs 2–9)

TYPE MATERIAL: The holotype, MGWUW ZI/57/215/a–b, is a part and counterpart of a well preserved, nearly complete articulated skeleton. Paratypes include: MGWUW ZI/57/214/a–b, ZI/57/171/1/a–b, as part and counterpart, and ZI/57/182 in a single plate (three specimens).

TYPE LOCALITY: Jamna Dolna near Bircza, Podkarpackie Voivodeship (Subcarpathian Province) of south-eastern Poland, Outer Carpathians, Poland.

TYPE HORIZON: Rudawka Tractionite Member of the Menilite Formation, Lower Oligocene, Rupelian, nannoplankton zone NP23.

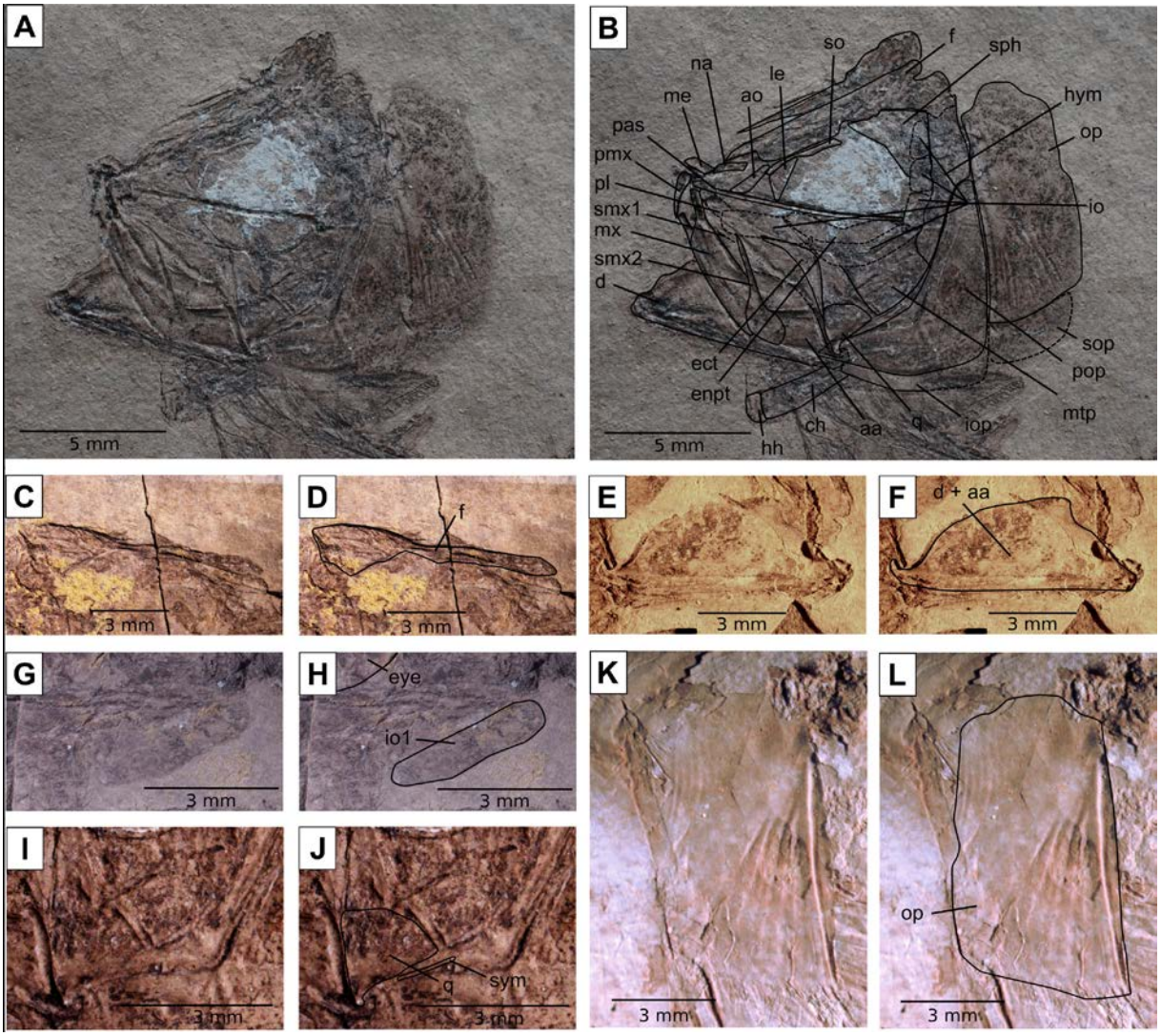


Text-fig. 2. †*Sanalosa janulosa* gen. et sp. nov. from the Oligocene of the Outer Carpathians, SE Poland. A – holotype, MWGUW ZI/57/215/a; B – paratype, MWGUW ZI/57/171/1/a; C – MWGUW ZI/57/219.

DERIVATION OF NAME: Named in honour of the Polish poet Janusz Szuber (1947–2020) from Sanok city, located close to the type locality, added to the reduced word *Alosa*.

DIAGNOSIS: Same as for genus.

ADDITIONAL MATERIAL: MWGUW ZI/57/133, ZI/57/219; ZPALWr. N/6407 (see Table 1).



Text-fig. 3. †*Sanalosa janulosa* gen. et sp. nov., skull and its details. A, B – Skull, paratype, MWGUW ZI/57/171/1/a; photo and superimposed interpretative drawing. C, D – Frontal, paratype, MWGUW ZI/57/182; photo and superimposed interpretative drawing. E, F – Lower jaw, paratype, MWGUW ZI/57/182, photo and superimposed interpretative drawing, anterior to the right. G, H – 1st infraorbital, paratype, MWGUW ZI/57/182, photo and superimposed interpretative drawing, anterior to the right. I, J – Quadrate and symplectic, paratype, MWGUW ZI/57/171/1/a, photo and superimposed interpretative drawing. K, L – Opercle, holotype, MWGUW ZI/57/214/a, photo and interpretative drawing. Abbreviations: aa – anguloarticular; ao – antorbital; ch – ceratohyal; d – dentary; ect – ectopterygoid; f – frontal; hh – hypohyal; hym – hyomandibular; io – infraorbital; iop – interopercle; enpt – endopterygoid; le – lateral ethmoid; me – mesethmoid; mtp – metapterygoid; mx – maxilla; na – nasal; op – opercle; pas – parasphenoid; pl – palatine , pmx – premaxilla; pop – preopercle; q – quadrate; smx – supramaxilla; so – supraorbital; sop – subopercle; sph – sphenotic; sym – symplectic.

MEASUREMENTS: See Table 2.

DESCRIPTION: Small fishes with a moderately high, elongated and laterally compressed body (Text-fig. 2); the smallest specimen is 46 mm standard length (SL) and the largest is 96 mm SL. The head is triangular in lateral view, its length is 23–40% SL. The mouth is small and terminal. The lower jaw articulation is located under the posterior part of the orbit (Text-fig. 3). The belly is moderately convex. The abdominal scutes form a very distinctive keel. Both pre- and postpelvic scutes are well-developed, present from the coracoid to almost the beginning of the anal fin and situated along the ventral margin.

Neurocranium. The neurocranium is elongated and triangular in lateral outline. Paired frontals are

Table 2. Morphometric characteristics of †*Sanalosa janulosa* gen. et sp. nov. Measurements are given in millimetres (mm) and as a percentage of the standard length, SL (in parentheses).

Morphometric character	MWGUW ZI/57/215/a holotype	MWGUW ZI/57/171/1/b paratype	MWGUW ZI/57/182 paratype	MWGUW ZI/57/214/a paratype	MWGUW ZI/57/133	MWGUW ZI/57/219	ZPALWr. N/6407	Studied material
Standard length [SL]	55	46	–	65	50	96	62	50–96
Head length	19 (35)	13 (28)	13 (–)	15 (23)	20 (40)	28 (29)	17 (27)	13–28 (23–40)
Maximum body depth	18 (33)	11 (24)	13 (–)	19 (29)	10 (20)	34 (35)	18 (30)	10–34 (20–35)
Predorsal distance	28 (51)	23 (50)	23 (–)	30 (46)	26 (52)	44 (46)	29 (48)	23–44 (46–52)
Prepelvic distance	31 (56)	26 (57)	–	31 (48)	–	49 (51)	30 (49)	26–49 (48–57)
Preanal distance	41(75)	34 (74)	–	53 (82)	–	74 (77)	48 (77)	34–74 (74–82)

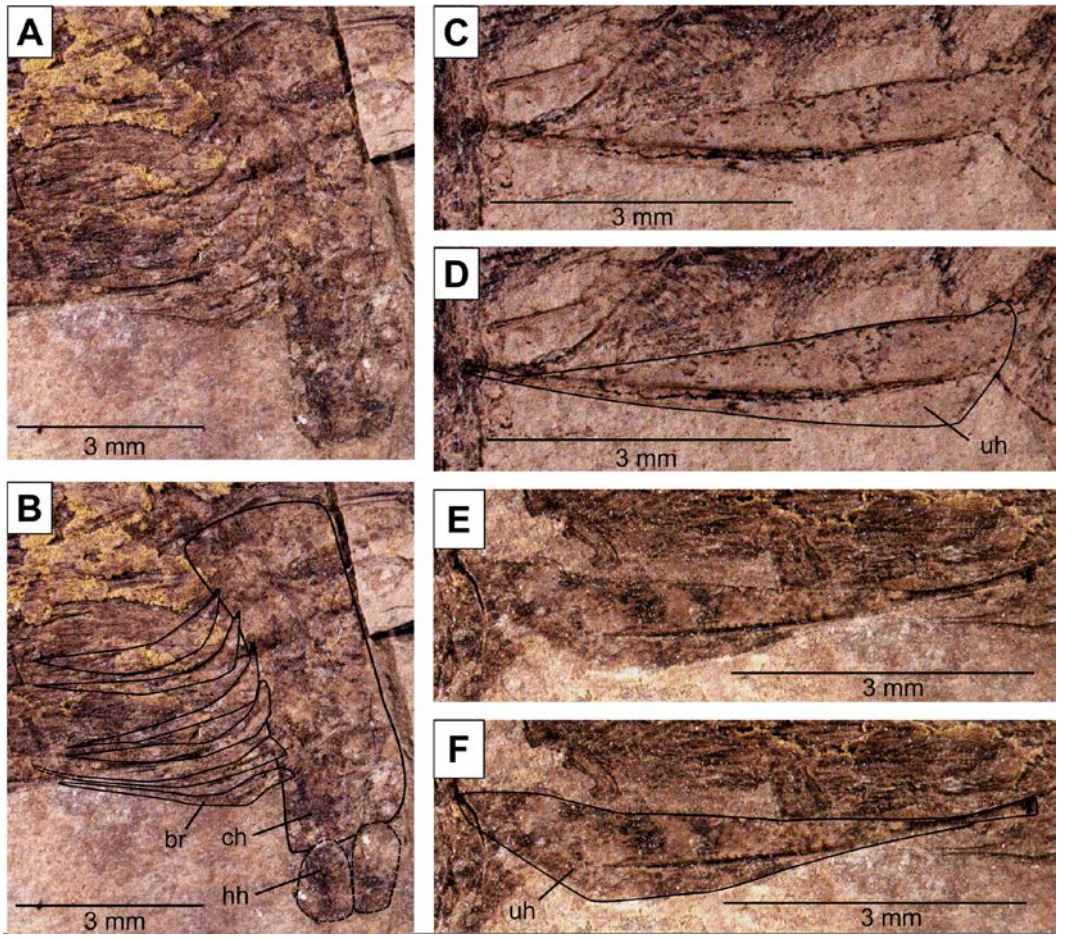
the largest bones in the skull roof. They are pointed anteriorly, wider posteriorly and narrow anteriorly; the bones are curved with the descending anterior part. In the posterior part, the frontals are sculptured with several slightly curved frontoparietal striae (Text-fig. 3C, D). Most of the frontals in the specimens studied are slightly compressed dorsoventrally, which allows us seeing both right and left bone simultaneously. The parasphenoid is long, thin, straight in its central part, being slightly curved posterodorsally and anteroventrally. The parietal, the supraoccipital and the epioccipital are poorly visible posteriorly to the posterior margin of frontals. The dorsal margin of the parietal articulates with the ventral margin of frontals. The pterotic is not preserved in the studied material, and the sphenotic region is poorly preserved. The orbitosphenoid is a moderately long, descending anteriorly and extending from above the central part of the orbit. The pterosphenoid is slightly dorsally convex. The triangular lateral ethmoid articulates with the anterior part of the frontals.

Circumorbital series. The nasal is small and moderately elongated. The supraorbital extends from above the central part of the orbit. The infraorbitals are poorly preserved; the first of them, ventral to the anterior part of the orbit, appears to be the largest bone of the series. The bone margins are poorly preserved, but they cover a large portion of the skull. The sclerotic ring is poorly preserved, its posterior part is not preserved but the anterior part appears to have a crescent moon shape.

Oral jaws and dentition. The premaxilla is toothless and slightly curved in lateral view. The maxilla is narrow anteriorly and high posteriorly. Its ventral margin is slightly convex and toothless. The anterior, narrow part is moderately long and only slightly curved. Two supramaxillae are present. The anterior part of the asymmetrical second supramaxilla is narrow and straight, while its posterior part is robust. Dorsal and ventral margins of the posterior part of the bone are convex and rounded. The first supramaxilla appears to be a thin, straight bone. The hypomaxilla is absent. The lower jaw is articulated with the skull beneath the posterior part of the orbit, and this articulation does not reach the vertical of the posterior margin of the orbit. The anterior edge of the lower jaw is moderately protruding. The lower jaw (toothless dentary together with the anguloarticular) is subtrapezoid (Text-fig. 3E, F), its ventral margin is straight, and the dorsal margin is slightly convex. The anteroventral edge of the jaw is rounded. The anguloarticular has a moderately developed articular process.

Suspensorium. The palatine seems to be long and narrow. The ectopterygoid forms an obtuse angle in its mid-length. The metapterygoid articulates anteriorly with the quadrate. The latter is triangular, with a thick ventral margin; its articulation with the lower jaw is located on the anteroventral corner. The symplectic (Text-fig. 3I, J) is thin and gracile. The hyomandibula is poorly preserved in the material studied, it is almost parallel to the vertical posterior margin of the orbit.

Opercular region. The preopercle is low, its horizontal ramus is considerably shorter and wider than the vertical one. The dorsal margin of the vertical ramus reaches the middle of the orbit. The angle between the preopercular rami is considerably greater than 90º. The preopercle has a smooth surface except for the canal-bearing ridges in the central part of the bone between the rami. Margins of the bone are rounded. The opercle is high and moderately wide, sculptured with 6–12 thin radial ridges (Text-fig. 3K, L). The ridges almost reach the ventral and caudal margins of the bone. The anterior margin is straight and slightly convex in the middle part. Parallel to the margin, there is a thick slightly convex ridge. The dorsal margin is convex, with a descending posterodorsal corner. The posterior margin is convex, with a slight incision in its upper part. The ventral margin is straight anteriorly and considerably rounded posteriorly. The subopercle

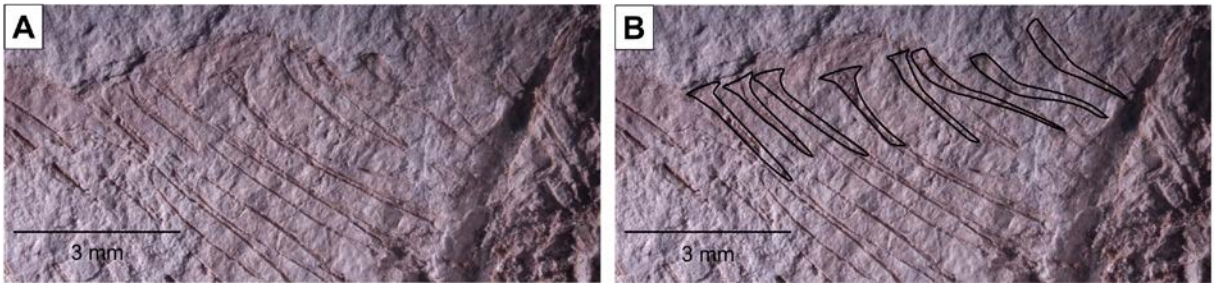


Text-fig. 4. †*Sanalosa janulosa* gen. et sp. nov., hyoid and branchial arches. A, B – Branchiostegal rays, paratype, MWGUW/57/182, photo and superimposed interpretative drawing. C, D – Urohyal, paratype, MWGUW/57/171/1/a, photo and superimposed interpretative drawing. E, F – Urohyal, paratype, MWGUW/57/182, photo and superimposed interpretative drawing. Abbreviations: br – branchiostegal rays; ch – ceratohyal; hh – hypohyal; uh – urohyal.

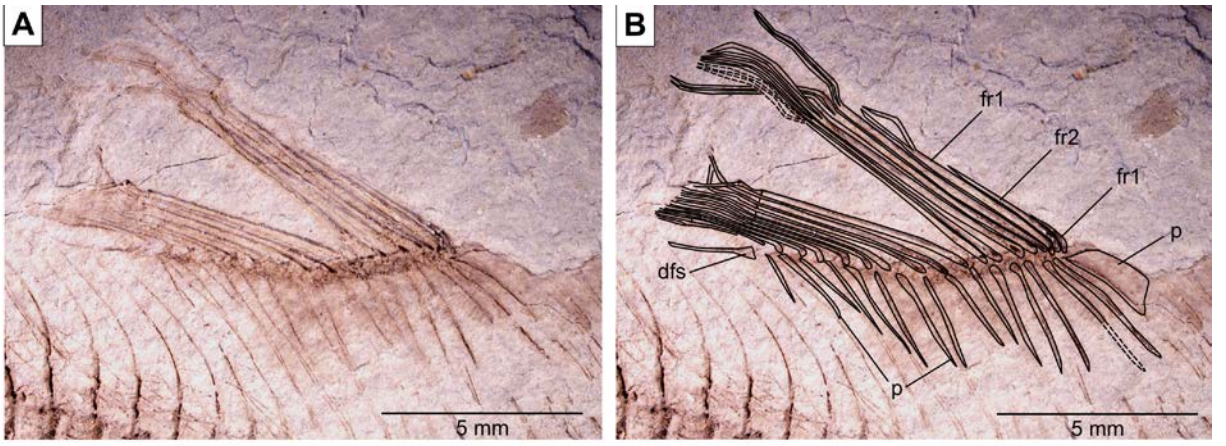
articulates with the ventral margin of the opercle; its ventral margin is rounded and convex. The subopercle process is not visible. The interopercle appears to be long and slightly curved.

Hyoid and branchial arches. There are 6–7 branchiostegal rays (Text-fig. 4). Both anterior and posterior rays are long, with thin and delicate anterior ones and posterior ones being wider. The last ray is higher than the others. The urohyal is feather-shaped, with a narrow and long anterior part. The bone is the highest in its central part. The ventral margin of the anterior part of the urohyal is prolonged onto the posterior part in a form of a ridge. The posterior part is rounded with the posterodorsal corner ascending. The dorsal margin appears to be slightly curved in the anterior part and straight in the posterior part. The hyoid bar and the margin between the dorsal and ventral hypohyals are poorly preserved in the material studied.

Vertebral column, ribs, and intermuscular bones. The vertebral column consists of 42–44 vertebrae including 17–18 caudal ones. Three anterior abdominal vertebrae are covered with an opercle. The first preural centrum is triangular in lateral view. In the caudal region, neural spines are slightly curved and positioned at approximately 45º to the vertebrae centrum; haemal spines are positioned similarly. There are 21–22 pairs of thin and long ribs reaching the dorsal margin of abdominal scutes. At least two series of intermuscular bones are visible throughout the abdominal part of the spine, including two ones in the caudal region. Intermuscular bones are delicate and curved, especially in the abdominal region; one series is short and close to the vertebrae centra, clearly



Text-fig. 5. †*Sanalosa janulosa* gen. et sp. nov., supraneurals. A, B – Holotype, MWGUW/57/215/a, photo and superimposed interpretative drawing.



Text-fig. 6. †*Sanalosa janulosa* gen. et sp. nov., dorsal fin. A, B – Holotype, MWGUW/57/215/a, photo and superimposed interpretative drawing. Abbreviations: dfs – dorsal fin stay; fr – fin rays; p – pterygiophores.

visible in the abdominal region. The series near the neural spines are closer to the vertebrae column than the series near the haemal spines.

Eight to ten supraneurals are present, they are curved and nail-shaped with the dorsal part wider and narrowing right after the wide dorsal margin (Text-fig. 5). They are positioned between the posterior margin of the skull and beginning of the dorsal fin. The latter is located slightly anteriorly to the middle of the body, originating above the 14th to 18th vertebrae, and terminating above the 23rd to 25th vertebrae.

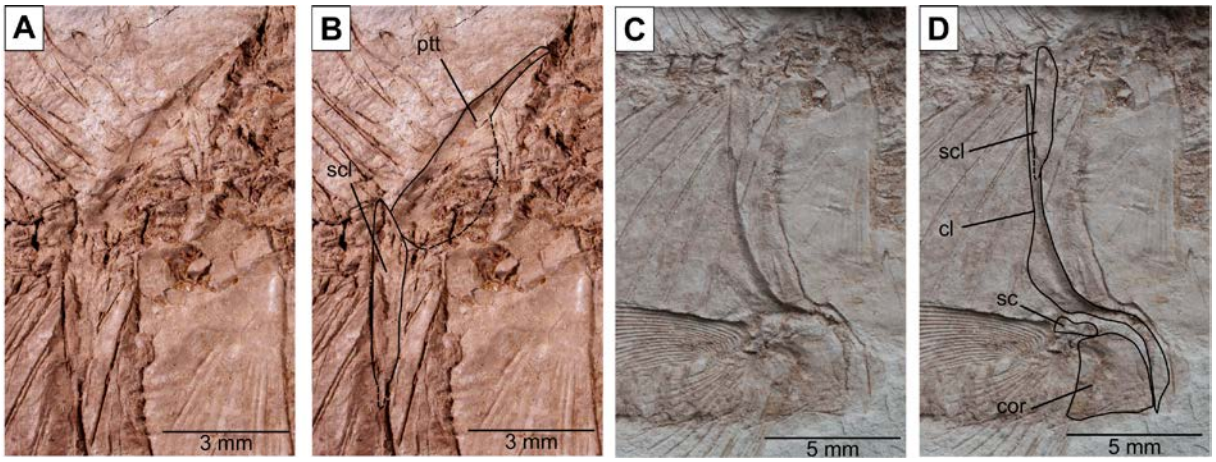
Dorsal fin. The dorsal fin is triangular and consists of 18–22 rays, the first anterior ray is the shortest (Text-fig. 6). There are at least 17 pterygiophores. The last pterygiophore is modified to a slender, horizontally oriented stay, which has the length of at least 3 vertebrae.

Paired fins and girdles. The posttemporal is elongate and subtriangular. The pectoral fins are long and positioned just slightly above the abdominal outline. They consist of 17–21 rays. The first rays are the longest. Two rod-like postcleithra are present. The supracleithrum is curved posteriorly; margin between the supracleithrum and cleithrum is below the vertebral column. The S-shaped cleithrum is the longest bone in the pectoral girdle; it reaches the anterior margin of the coracoid which is subquadrate in lateral view (Text-fig. 7).

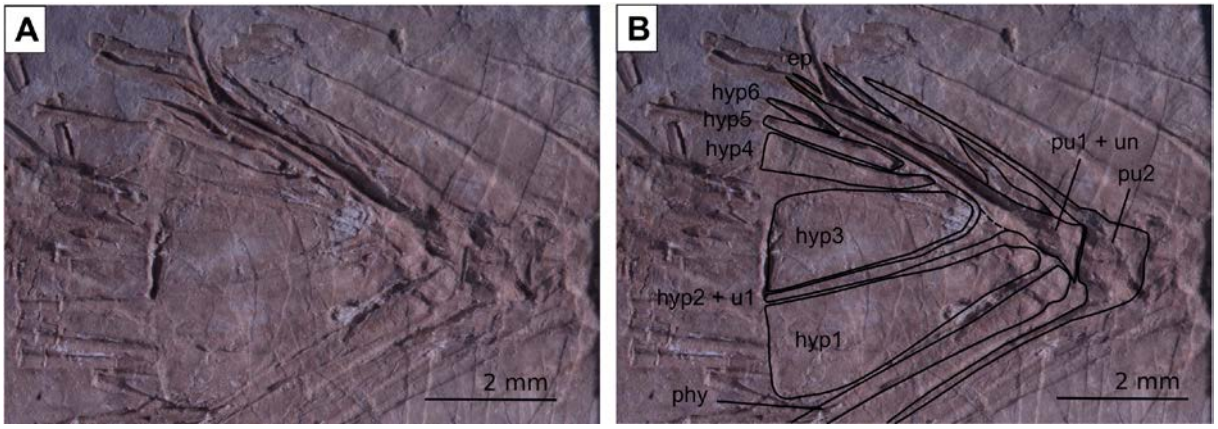
The pelvic fins are positioned beneath the middle or anterior part of the dorsal fin with the length of 5–6 vertebrae. They originate below the 18th–19th vertebrae. The pelvic bone is triangular in lateral view with the length of 4–5 vertebrae, pointing anteriorly but poorly visible because of the abdominal scutes. The pelvic fin consists of 8 rays.

Anal fin. The anal fin consists of 21–23 rays and has 20–22 pterygiophores. It originates below the 27th–33rd vertebrae and terminates above the 38th–42nd vertebrae. Rays closer to the caudal fin are displaced. The first ray is shorter than the others. The last two rays are not elongated.

Caudal fin and skeleton. The caudal fin is forked and deeply notched. Six hypurals are present and two epurals are visible (Text-fig. 8). The second hypural



Text-fig. 7. †*Sanalosa janulosa* gen. et sp. nov., pectoral girdle. A–D – Holotype, MWGUW/57/215/a, photo and superimposed interpretative drawing. Abbreviations: cl – cleithrum; cor – coracoid; ptt – posttemporal, sc – scapula; scl – supracleithrum.



Text-fig. 8. †*Sanalosa janulosa* gen. et sp. nov., caudal skeleton. A, B – Details of the caudal skeleton, paratype, MWGUW ZI/57/214/a, photo and superimposed interpretative drawing. Abbreviations: ep – epural; hyp – hypural; np – neural plate; phy – parhypural; pu – preural centrum; un – uroneural.

seems to be fused with the first ural centrum. The first preural vertebrae bears a short and thin neural plate. The parhypural is long and higher in the anterior part. The fin has 20 principal rays (I, 9 + 9, I) and about 11 procurrent rays.

Squamation. Large cycloid scales with parallel grooves (Text-fig. 9A–F).

Abdominal scutes. A continuous series originates anterior to the pectoral fins and terminates anterior to the anal fin. Scutes in the gular region, prepelvic and postpelvic ones are well-developed (Text-fig. 9G, H). The prepelvic scutes are larger. The ventral margin of each scute is descending posteriorly and forms a distinctive keel. There are at least 3 to 5 scutes along the gular region (free prepelvic scutes), 11–14 prepelvic scutes associated with the ribs and at least 11–12 postpelvic ones. The uncertainty in the meristic data regarding the abdominal scutes is because the pectoral fins might cover some of the scutes, and scutes near the anal fin might have been displaced. The pelvic scute is the largest as compared to the others.

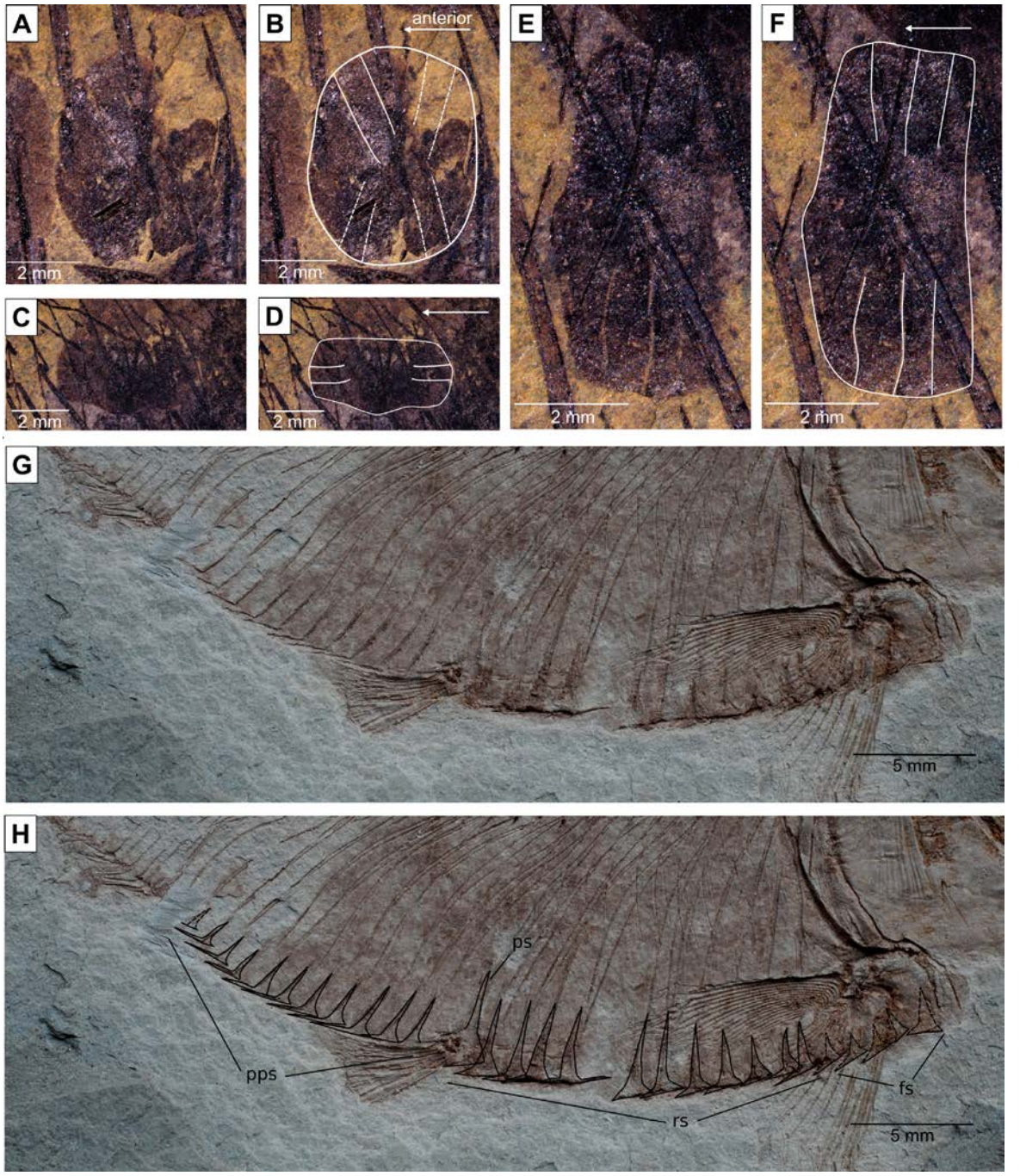
DISCUSSION

Systematic discussion

The osteological and meristic data (Table 3) support the assignment of the examined specimens from the Oligocene of the Polish Outer Carpathians to a new genus and species of the Family Alosidae in the Order Clupeiformes.

Table 3. Summary of selected morphological characters used to discriminate selected genera and species of the Order Clupeiformes. *Abdominal scutes formula: [prepelvic scutes; pospelvic scutes] unassociated free scutes in the gular region; rib–associated prepelvic scutes scutes; scutes between the coracoid and pelvic fin; scutes behind the pelvic fin. Comparative information is derived from Daniltshenko (1960, 1968, 1980), Grande (1982, 1985), Whitehead (1985), Murray *et al.* (2005), Baykina (2012, 2013), Marramà and Carnevale (2015a, b, 2018), Baykina and Schwarzhans (2017a, b), Kovalchuk *et al.* (2020), Kevrekidis *et al.* (2021), Fricke *et al*. (2024), Froese and Pauly (2024), and Granica *et al*. (2024).

Taxon	Frontoparietal striae	Opercle	Branchiostegal rays	Supraneurals	Dorsal scutes	Hypomaxilla	Dorsal-fin pterygiophores or rays (rays)	Anal-fin pterygiophores or rays (rays)	Pectoral-fin rays	Pelvic-fin rays	Vertebrae	Abdominal scutes *
†*Sanalosa janulosa*	present	striations	6–7	8–10	0		17 (18–22)	20–23 (21–23)	17–21	8	42–44	[15–17; 11–12] 3–5; 11–14; 11–12
Alosa (extant)		striations	7–8	9–13	0–1		15–22	15–27	14–18	9–11	47–60	
Alosa algeriensis		striations					(18–22)	(20–25)		9	53–57	33–39 [19–23; 13–16]
Alosa fallax		striations					(16–22)	(19–26)	15–17	9	49–59	32–41 [18–23; 12–18]
†*Alosa genuina*		striations					(15–17)	(17–18)	14–15	9	39–40	[12; 8]
†*Alosa sculptata*		striations					(14)	(18–19)	17	7–8	44	[15; 14]
†*Alosa* cf. *sagorensis*		striations					(15)	(20)	15–16	8	39–41	22–24
†*Beksinskiella*	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; 10–11; 10–11
Brevoortia		striations	7	10–12			17–24	18–24		7	45–48	about 30–32
†*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	23–32
Dussumieria			12–17	21–22			19–22	14–18	12–15	8	55–56	0; 0; 0
†*Eoalosa*		smooth		13+	0		15	17		7	47	0; 12; 5
†*Gosiutichthys*		smooth	7–8	6–7	12–13	absent	10–11	10–13		6–7	34–36	20–22
†*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	about 21–23
†*Maicopiella*	absent	smooth	7	8–10	0	absent	19	17–18	17	8–9	42–45	0; 14–15; 10–11
†*Moldavichthys*	present	smooth	7–8	9–10	0		16–17	17–18	?	8	39–44	[15–16; 8]
Opisthonema		smooth	6	7–9	1	absent	18–19	18–22	?	8	45–47	
†*Paretrumeus*		smooth					(15–17)	(7–8)	20–23	26–27	50–55	0; 0; 0
†'*Pomolobus*'		striations			0		14–17	17–22	14–18	8–9	40–43	[10–13; 9–12]
†'*Pomolobus*' *curtus*		striations					(14–15)	(19–20)	14–15	9	40–41	[11–12; 9–10]
†'*Pomolobus*' *facilis*		striations					(16–17)	(20–22)	17–18	8–9	42–43	[10–11; 12]
†'*Pomolobus*' *antiquus*		striations					(14–15)	(17–18)	17	9	42	[12–13; 9–10]
†*Primisardinella*		smooth		9–10	0	absent	15–16	13–15		8	39–40	3–4; 10–11; 9–10
†*Pseudohilsa*	present	smooth	5	10–11	0	absent	(10–17)	(16–19)	15	8–9	36–42	4; 11–12; 10–11
†*Rupelia*	present	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	
†*Sardina necteodosciobanensis*		striations					(16–18)	(20)	18–19	9	46–47	[12–13; 12–13]
†*Sardina tarletskovi*		striations		11			15–16 (14–15)	14			47–49	[17–18; 13]
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
Sprattus		smooth	7	15–17	0	absent	17–18	16–19		7–8	45–48	
†*Trollichthys*		smooth		5–6			14–16	13		8	41–42	0; 0; 0



Text-fig. 9. †*Sanalosa janulosa* gen. et sp. nov., scales and abdominal scutes. A, B – Details of a scale from the anterior median region of the body, MWGUW/57/219, photo and superimposed interpretative drawing. C, D – Details of a scale from the anterior dorsal region of the body, MWGUW/57/219, photo and superimposed interpretative drawing. E, F – Details of a scale from the median region of the body, MWGUW/57/219, photo and superimposed interpretative drawing. G, H – Details of abdominal scutes, holotype, MWGUW/57/215/a, photo and superimposed interpretative drawing. Abbreviations: fs – un-associated free scutes in the gular region; ps – pelvic scute; pps – postpelvic scutes, scutes behind the pelvic fin; rs – rib-associated prepelvic scutes.

The presence of abdominal scutes (keeled scales along the ventral midline) indicates that †*Sanalosa janulosa* gen. et sp. nov. belongs to the Clupeiformes (see Wang *et al.* 2022). The fusion of the second hypural with the first ural centrum, a separated 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 indicate that the species belongs to the Suborder Clupeoidei (see Grande 1985). The opercle sculptured with radial ridges supports its inclusion within the Family Alosidae (see Wang *et al.* 2022).

Comparison with extant genera

†*Sanalosa* gen. nov. differs from extant genera of the Clupeiformes except of *Alosa*, *Brevoortia*, *Sardina*, and *Sardinops* (see Grande 1985; Whitehead 1985; Wang *et al.* 2022) by the opercle sculptured with radial ridges. It differs from *Alosa*, *Brevoortia*, *Sardina*, and *Sardinops* (Grande 1985; Whitehead 1985; Froese and Pauly 2024) by having a lesser number of vertebrae (42–44 *vs*. 47–60, 45–48, 50–51 and 50–52, respectively). It differs in the number of rays of the pelvic fin from *Alosa* and *Brevoortia* (8 *vs*. 9–11 and 7, respectively). †*Sanalosa* gen. nov. can be differentiated from the genus *Alosa* by the position of the lower jaw articulation with the skull – it does not reach the vertical of the posterior margin of the orbit whereas the lower jaw articulation in *Alosa* is behind this vertical axis. †*Sanalosa* gen. nov. has a smaller number of supraneurals compared to *Brevoortia*, with the highest number the same as the smallest number of supraneurals in *Brevoortia* (8–10 *vs*. 10–12). †*Sanalosa* gen. nov. differs from *Sardina* in a higher number of pterygiophores of the anal fin (20–23 *vs*. 17–19).

The urohyal of *Sardinops* (see Sato *et al.* 1988) has a longer and higher anterior part of the bone than that in †*Sanalosa* gen. nov. The respective bone of *Sardinops* has a curved dorsal margin and a more paddle-like outline. The urohyal of †*Sanalosa* gen. nov. has a straighter dorsal margin and more feather-like outline.

Comparison with extinct genera and species

†*Sanalosa* gen. nov. differs from extinct genera of the Clupeiformes (e.g., †*Beksinskiella* Granica, Bienkowska-Wasiluk and Pałdyna, 2024; †*Bolcaichthys* Marramà and Carnevale, 2015a, †*Chasmoclupea* Murray, Simons and Attia, 2005, †*Eoalosa* Marramà and Carnevale, 2018, †*Gosiutichthys* Grande, 1982, †*Karaganops* Baykina and Schwarzhans, 2017a, †*Knightia* Jordan, 1907, †*Maicopiella* (Menner, 1949), †*Paretrumeus* Daniltshenko, 1980, †*Primisardinella* Daniltshenko, 1968, †*Pseudohilsa* Menner, 1949, †*Rupelia* Baykina and Kovalchuk in Kovalchuk *et al.* 2020, †*Sarmatella* Menner, 1949, and †*Trollichthys* Marramà and Carnevale, 2015b except of †'*Pomolobus*' Rafinesque, 1820 and †*Moldavichthys* Baykina and Schwarzhans, 2017b by the opercle sculptured with radial ridges (see Table 3). †*Sanalosa* gen. nov. differs from the Eocene †*Trollichthys* Marramà and Carnevale, 2015b, and †*Paretrumeus* Daniltshenko, 1980 in the presence of abdominal scutes.

The Miocene species †*Moldavichthys switshenskae* (Baykina and Schwarzhans, 2017b) differs from †*Sanalosa janulosa* gen. et sp. nov. by fewer rays in the dorsal fin (15–16 *vs*. 18–22), pectoral fins (14–16 *vs*. 17–21) and the anal fin (17–18 *vs*. 21–23), as well as the smaller number of postpelvic abdominal scutes (8 *vs*. 11–12). The new genus and species has a different morphology of the preopercle. The horizontal ramus is slightly shorter, and the vertical ramus is narrower. Another difference is the presence of the teeth: the maxilla of †*M. switshenskae* is serrated and there are teeth on the premaxilla and dentary. The Oligocene †'*Pomolobus*' *curtus* Daniltshenko, 1960 differs from †*S. janulosa* gen. et sp. nov. by fewer rays in the dorsal fin (14–15) and the pectoral fins (14–15). †*Sanalosa janulosa* gen. et sp. nov. can be differentiated from the Oligocene †'*Pomolobus*' *facilis* Daniltshenko, 1960 and †'*P.*' *antiquus* (Smirnov, 1936) by having more numerous rays in the dorsal fin (18–22 *vs*. 16–17; 14–15, see Daniltshenko 1980). Those three species also have fewer prepelvic abdominal scutes (11–12; 10–11; 12–13 *vs*. 15–17 including 3 to 5 in the gular region).

The Oligocene †*Beksinskiella longimana* (see Granica *et al*. 2024) differs from †*S. janulosa* gen. et sp. nov. by its different preopercle morphology (both rami are similar in length *vs*. the horizontal ramus is shorter than the vertical one). The urohyal of †*B. longimana* becomes higher in the central part of the bone at one point, while the height of this bone in †*Sanalosa* gen. nov. changes gradually. The posterior margin of the urohyal is fully rounded in †*B. longimana*. The posterior part of the bone in †*B. longimana* retains a similar height, while the height in the urohyal of †*Sanalosa* gen. nov. in the posterior part becomes smaller towards its dorsal margin. †*Beksinskiella longimana* has poorly developed postpelvic scutes, and their number is smaller (about 8), while †*S. janulosa* has more numerous (11–12) and well-developed ones.

The Oligocene †*Sardina necteodosciobanensis* Ciobanu, 1977 differs from †*S. janulosa* gen. et sp. nov. by its having fewer rays in the dorsal fin (16–18), more rays in pelvic fins (9) and more vertebrae (46–47). The Miocene †*Sardina tarletskovi* Baykina, 2015 differs from †*S. janulosa* gen. et sp. nov. by its

having fewer rays in the anal fin (15) and in the dorsal fin (14–15). †*Sardina tarletskovi* has more numerous vertebrae (47–49). It also has a smaller head (22% SL). †*Sanalosa janulosa* gen. et sp. nov. has more dorsal fin rays (18–22) than the Oligocene–Miocene †*Alosa genuina* Daniltshenko, 1960 (15–17), †*Alosa sculptata* Weiler, 1928 (14) and †*Alosa* cf. *sagorensis* Steindachner, 1863 (15) (see Weiler 1933, 1938; Ciobanu 1977; Daniltshenko 1980). The sculpture on the opercle in †*S. janulosa* covers a smaller area than that in †*A.* cf. *sagorensis* (see Weiler 1933).

Distribution, diversity and palaeobiogeography of the Oligocene Clupeiformes

The earliest clupeiform fish in the fossil record, preserved as skeleton, has been reported from the Lower Cretaceous of Brazil (De Figueiredo 2009), dated to approximately 126–121 Ma (Barremian, calibrated Geological Time Scale after Gradstein *et al.* 2020).

During the Oligocene, representatives of this order were abundant in marine ecosystems, which is indicated by their rich fossil record and high percentage in fossil assemblages (Kotlarczyk *et al.* 2006; Bienkowska-Wasiluk 2010; Přikryl *et al.* 2016).

More than twenty clupeiform taxa, preserved as skeletons, have been reported from the Czech Republic, Egypt, Hungary, Poland, Romania, Russia, and Ukraine (Weiler 1933; Ciobanu 1977; Daniltshenko 1980; Murray *et al.* 2005; Kovalchuk *et al.* 2020; Granica *et al.* 2024), although recent investigations (e.g., Kovalchuk *et al.* 2020) show that revisions of some previously described taxa led to a reduced number of species.

†*Alosa sculptata* has been recorded from Romania (Ciobanu 1977) and Germany (Weiler 1928), although some morphological characters of the species have not been described (e.g., the number of supraneurals, epurals and branchiostegal rays), therefore the validity of this species needs to be reconsidered.

†*Alosa* cf. *sagorensis* has been identified from Hungary (Weiler 1933, 1938) and Poland (Szymczyk 1978), but the Polish specimens are fragmentary and a complete skeleton has not been found yet. Similarly to †*A. sculptata*, the validity of this species needs to be reconsidered due to the absence of important morphological characters in the original description. †*Alosa sagorensis* has been described from the Miocene of Croatia (Steindachner 1863).

†*Beksinskiella longimana* (Heckel, 1850) has been recorded from the Czech Republic, Poland, and Ukraine (Granica *et al.* 2024)

†*Chasmoclupea aegyptica* Murray, Simons and Attia, 2005 has been described from the freshwater deposits of Egypt (Murray *et al.* 2005).

†*Moldavichthys switshenskae* from the Miocene of Moldova (Baykina and Schwarzhans, 2017b) is one of the earliest species of the Alosidae that has a well-documented morphology. However, more than 6 taxa of putative Alosidae occurred earlier than *Moldavichthys* in the Oligocene.

†'*Pomolobus*' *antiquus*, †'*P.*' *curtus*, and †'*P.*' *facilis* have been described from Russia (Daniltshenko 1960). *Pomolobus* is currently regarded as a synonym of *Alosa* (Fricke *et al.* 2024). These three species share some characters with *Alosa* but differ in having fewer vertebrae and abdominal scutes. Their revision would be desirable to clarify their taxonomic status.

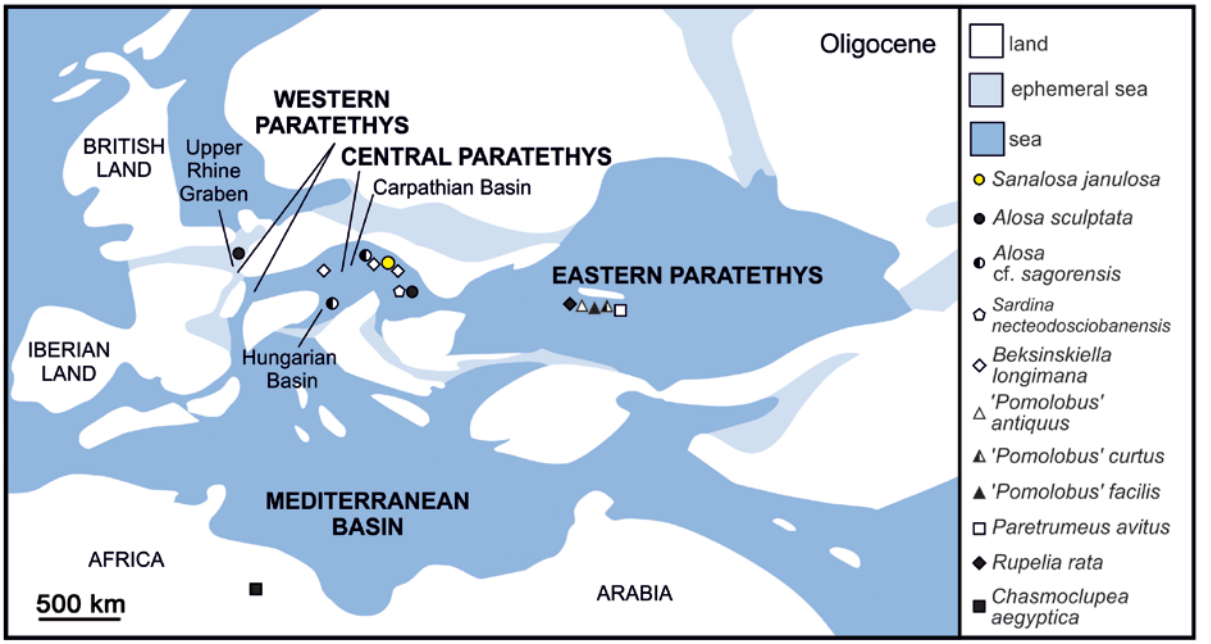
†*Rupelia rata* (Daniltshenko, 1959) is known from Russia (Kovalchuk *et al.* 2020), as well as the putative Dussumieriidae, †*Paretrumeus avitus* Daniltshenko, 1980.

†*Sardina necteodosciobanensis* has been described from Romania (Ciobanu 1977).

All the above species with the exception of †*Ch. aegyptica* inhabited marine environments.

The Miocene fossil record of the Clupeiformes within the Paratethys is represented mostly by species which are different from the Oligocene ones, with only one or two species (†*Alosa* cf. *sagorensis*, †*Beksinskiella longimana*) found to be present in both series. This could be a result of significant environmental changes in the Paratethys including sea-level rise and drop, periodical isolation of its sub-basins and tectonic events (e.g., Kotlarczyk *et al.* 2006; Kováč *et al.* 2016, 2017; Sachsenhofer *et al.* 2017).

Clupeiform fossils have been reported from the Oligocene of Western, Central and Eastern Paratethys (e.g., Kotlarczyk *et al.* 2006; Maxwell *et al.* 2016; Kovalchuk *et al.* 2020). In the Western Paratethys, in the Upper Rhine Graben lived †*Alosa sculptata* (see Weiler 1928). This species was present also in the Central Paratethys in the Carpathian Basin together with †*Alosa* cf. *sagorensis*, †*Beksinskiella longimana,* †*Sanalosa janulosa* gen. et sp. nov., and †*Sardina necteodosciobanensis*. †*Alosa* cf. *sagorensis* lived also in the Hungarian Basin of the Central Paratethys (see Weiler 1933). The clupeiform assemblage of Eastern Paratethys included †*Paretrumeus avitus*, †'*Pomolobus*' *antiquus*, †'*P.*' *curtus*, †'*P.*' *facilis*, and †*Rupelia rata* (see Daniltshenko 1980; Kovalchuk *et al.* 2020), all of which were absent in the Central and Western Paratethys. †*Chasmoclupea aegyptica* inhabited the rivers of North Africa (Murray *et al.* 2005).



Text-fig. 10. Paleobiogeography of representatives of the Order Clupeiformes in the Oligocene based on skeleton findings; palaeogeography adopted from Popov *et al.* (2002).

Although a number of fish taxa lived both in the Central and Eastern Paratethys during Oligocene (e.g., Bannikov 2010; Barkaszi and Kovalchuk 2021; Kovalchuk and Barkaszi 2021; Přikryl *et al.* 2022), the composition of the clupeiform assemblages differed considerably in these parts of the Paratethyan realm (Text-fig. 10). All Eocene genera from the Tethys, i.e., †*Bolcaichthys*, †*Eoalosa*, and †*Trollichthys* (see Marramà and Carnevale 2015a, b, 2018) were absent in the Paratethys during the Oligocene. No clupeiform genus has been recorded in the Peri-Tethys during the Eocene (see Daniltshenko 1980). Only *Alosa* and *Sardina* were present in the Paratethys during the Oligocene and Miocene. †*Alosa sculptata*, †*A.* cf. *sagorensis,* and †*Sardina necteodosciobanensis* lived during the Oligocene (see Weiler 1928, 1933; Ciobanu 1977), whereas †*A. sagorensis*, †*A. genuina,* and †*Sardina tarletskovi* lived during the Miocene (see Steindachner 1863; Daniltshenko 1980; Baykina 2015).

Other genera living in the Paratethys during the Oligocene, i.e., †*Beksinskiella*, †*Paretrumeus*, †'*Pomolobus*', †*Rupelia*, †*Sanalosa* gen. nov., and *Sardina* have not been recorded in the Miocene of the Paratethys. †*Karaganops*, †*Maicopiella*, †*Moldavichthys*, †*Pseudohilsa*, and †*Sarmatella* originated in the Paratethys during the Miocene. Although the clupeiform evolutionary history remains to be explored further, it is clear that they evolved rapidly during Eocene, Oligocene, and Miocene, and endemism prevailed in the Paratethys. Differences between the species of clupeiforms are expressed in meristic and osteological characters, but the taxa have a high number of shared characters. This concerns both recent and Paleogene–Neogene Clupeiformes in the northern part of the Tethys. Therefore comparison of taxa and recognition of evolutionary trends needs further comprehensive analyses. We believe that future investigations of clupeiform fossils from the former Tethys will improve our knowledge on the evolutionary history of this group.

CONCLUSIONS

Osteological, morphometric and meristic analyses of the clupeiform material from the Polish Outer Carpathians revealed a new genus and species, †*Sanalosa janulosa*. The description of †*S. janulosa* gen. et sp. nov. provides a substantial improvement to our knowledge of osteology of the Oligocene alosids, documenting essential features such as abdominal scutes, supraneurals, and urohyal. The newly described species existed in the Central Paratethys together with †*Alosa sculptata*, †*Alosa* cf. *sagorensis*, †*Beksinskiella longimana*, and †*Sardina nec-*

teodosciobanensis. Clupeiform assemblages were highly diverse in the basins of the Paratethyan realm, showing a rapid, often endemic evolution. We believe that our investigation will improve the knowledge on the evolutionary history of clupeiform fishes and can contribute to improving the palaeobiogeographic reconstructions of the Paratethys**.**

Acknowledgements

We express our gratitude to Marcin Pałdyna for discussions and collecting some specimens, Robert Szybiak for access to his specimens, Radosław Wasiluk for helping with fieldwork, Tomasz Praszkier and Krzysztof Dembicz for collecting some specimens. We acknowledge Bettina Reichenbacher and Werner Schwarzhans for their valuable comments and reviews that significantly improved the quality of the manuscript. The research of OK was supported by an individual grant 'The role of particular fish groups in the functioning of late Mesozoic and Cenozoic ecosystems of Eastern Europe' (No. 0123U102984) from the National Academy of Sciences of Ukraine.

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.

Arratia, G. 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. In: Arratia, G. and Schultze, H.-P. (Eds), Mesozoic Fishes 2 – Systematics and Fossil Record, 265–334. Verlag Dr. Friedrich Pfeil; München.

Bannikov, A.F. 2010. Fossil acanthopterygian fishes (Teleostei, Acanthopterygii). In: Tatarinov, L.P., Vorobyeva, E.I. and Kurochkin, E.N. (Eds), Fossil Vertebrates of Russia and Adjacent Countries, 1–244. GEOS; Moscow. [In Russian]

Barkaszi, Z. and Kovalchuk, O. 2021. New records of Oligocene selachians (Elasmobranchii) from the Outer Carpathian Basin. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **301** (2), 171–181.

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. 2015. A new species of the genus *Sardina* (Pisces, Clupeidae) from the Middle Miocene of the Eastern Paratethys. *Paleontological Journal*, **49**, 68–72.

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.

Bienkowska-Wasiluk, M. 2010. Taphonomy of Oligocene teleost fishes from the Outer Carpathians of Poland. *Acta Geologica Polonica*, **60** (4), 479–533.

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**, 1–276.

Ciobanu, M. 1977. Fauna fosilă din Oligocenul de la Piatra Neamț, 159 pp. Editura Academiei Republici Socialiste România; București.

Cuvier, G. 1817. Le Règne Animal distribué d'après son organization pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poisons, les mollusques et les annelids. Edition 1 (2), 532 pp. Déterville; Paris.

Daniltshenko, P.G. 1959. Lower Maikopian species of the genus *Sardinella*. *Paleontological Journal*, **1**, 95–97. [In Russian]

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, 113–156. In: Obruchev, 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, 7–26. In: Novitskaya, L.I. (Ed.), Bony fishes of the USSR. *Trudy Paleontologicheskogo Instituta AN SSSR*, **178**, 7–26. [In Russian]

De Figueiredo, F.J. 2009. A new clupeiform fish from the Lower Cretaceous (Barremian) of Sergipe-Alagoas Basin, northeastern Brazil. *Journal of Vertebrate Paleontology*, **29** (4), 993–1005.

FAO. 2022. The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation, 266 pp. FAO; Rome.

Fricke, R., Eschmeyer, W.N. and van der Laan, R. (Eds.) 2024. Eschmeyer's Catalog of Fishes: Genera, Species, References. Available at: http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp, accessed 20.08. 2024

Froese, R. and Pauly, D. 2024. FishBase. World Wide Web electronic publication. *www.fishbase.org*, version (02/2024).

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.

Gradstein, F.M., Ogg, J.G., Schmitz, M.D. and Ogg, G.M. 2020. Geologic Time Scale 2020, 1357 pp. Elsevier.

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.

Granica, M., Bienkowska-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.

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.

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

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** (3), 605–621.

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.

Kováč, M., Hudáčková, N., Halásová, E., Kováčová, M., Holcová, K., Oszczypko-Clowes, M., Báldi, K., Less, G., Nagymarosy, A., Ruman, A., Klučiar, T. and Jamrich, M. 2017. The Central Paratethys palaeoceanography: a water circulation model based on microfossil proxies, climate, and changes of depositional environment. *Acta Geologica Slovaca*, **9**, 75–114.

Kováč, M., Nagymarosy, A., Oszczypko, N., Ślączka, A., Csontos, L., Marunteanu, M., Matenco, L. and Marton, E. 1998. Palinspastic reconstruction of the Carpathian–Pannonian region during the Miocene. In: Rakus, M. (Ed.), Geodynamic Development of the Western Carpathians, 189–217. Slovak Geological Survey; Bratislava.

Kováč, M., Plašienka, D., Soták, J., Vojtko, R., Oszczypko, N., Less, G., Ćosović, V., Fügenschuh, B. and Králiková, S. 2016. Paleogene palaeogeography and basin evolution of the Western Carpathians, Northern Pannonian domain and adjoining areas. *Global and Planetary Change*, **140**, 9–27.

Kovalchuk, O.M. and Barkaszi, Z. 2021. Oligocene basking sharks (Lamniformes, Cetorhinidae) of the Carpathian Basin with a reconsideration of the role of gill rakers in species diagnostics. *Journal of Vertebrate Paleontology*, **41** (2), e1929269.

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.

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.

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** (6), e1014490.

Marramà, G. and Carnevale, G. 2015b. Eocene round herring from Monte Bolca, Italy. *Acta Palaeontologica Polonica*, **60** (3), 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, Neogene, 346–360. Gosgeolitizdat; Moscow. [In Russian]

Müller, J. 1846. Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. *Physikalisch-Mathematische Abhandlungen der königlichen Akademie der Wissenschaften zu Berlin*, **1846**, 117–216.

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, 707 pp. John Wiley and Sons; Hoboken, New Jersey.

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.

Přikryl, T., Kovalchuk, O., Carnevale, G. and Barkaszi, Z. 2022. New material of the puffer fish *Archaeotetraodon winterbottomi* Tyler et Bannikov, 1994 (Tetraodontidae) from the Oligocene of the Eastern Paratethys. *Fossil Imprint*, **79** (2), 513–518.

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

Sachsenhofer, R.F., Popov, S.V., Bechtel, A., Coric, S., Francu, J., Gratzer, R., Grunert, P., Kotarba, M., Mayer, J., Pupp, M., Rupprecht, B.J. and Vincent, S.J. 2017. Oligocene and Lower Miocene source rocks in the Paratethys: Palaeogeographic and stratigraphic controls. In: Simmons, M.D., Tari, G.C. and Okay, A.I. (Eds), Petroleum Geology of the Black Sea. *Geological Society of London, Special Publications*, **464**, 267–306.

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 from the Northern Caucasian Oligocene (Chernorech'e District). *Trudy Uzbekskogo gosudarstvennogo universiteta*, **5**, 1–92. [In Russian]

Steindachner, F. 1863. Beiträge zur Kenntnis der fossilen Fische Österreich. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe*, **40**, 128–142.

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.

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: 08.2024]

Weiler, W. 1928. Beiträge zur Kenntnis der tertiären Fische des Mainzer Beckens II. 3 – Teil: Die Fische des Septarientones. *Abhandlungen der Hessischen Geologischen Landesanstalt zu Darmstadt*, **8**, 1–63.

Weiler, W. 1933. Zwei oligozäne Fischfaunen aus dem Königreich Ungarn. *Geologica Hungarica, series palaeontologica*, **11**, 1–54.

Weiler, W. 1938. Neue Untersuchungen an mitteloligozänen Fischen Ungarns. *Geologica Hungarica, series palaeontologica*, **15**, 5–30.

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.

Żytko, K., Gucik, S., Oszczypko, N., Zając, R., Garlicka, I., Nemčok, J., Eliaš, M., Menčik, E., Dvorak, J., Stranik, Z., Rakuš, M. and Matejovska, O. 1989. Geological map of the Western Outer Carpathians and their foreland without Quaternary formations. In: Poprawa, D. and Nemčok, J. (Eds), Geological Atlas of the Western Carpathians and their Foreland. 1: 500 000. Państwowy Instytut Geologiczny; Warszawa.

Manuscript submitted: 13th May 2024
Revised version accepted: 16th September 2024