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Taxonomic revision of the Oligocene percoid fish *Oligoserranoides budensis* (HECKEL, 1856), from the Paratethys and paleobiogeographic comments

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ABSTRACT

Small perch-like fishes from the Oligocene of the Paratethys have been traditionally assigned to *Serranus budensis* (HECKEL, 1856). A morphological revision of the holotype and specimens previously assigned to *S. budensis* from the Outer Carpathians, Poland, is provided herein. They are re-assigned to the species *Oligoserranoides budensis* (HECKEL, 1856) — *Percoidei incertae sedis*. New specimens assigned to *Ol. budensis* from the Outer Carpathians, Poland, are introduced. Our results reveal that *Ol. budensis* is very similar to the species *Caucasoserranoides morozkiensis, Carpathoserranoides brnoensis, Carpathoserranoides polonicus*, and *Oligoserranoides comparabilis*, and further studies are necessary to revise the validity of those species. *Ol. budensis* shares many characters with genera *Lutjanus* and *Ocyurus* of the superfamily Lutjanoidea. *Ol. budensis* differs from Lutjanoidea in having a toothless palatine. The palaeobiogeography of Oligocene small perch-like fishes in the Paratethys is presented and discussed.

KEYWORDS **Teleostei. Perciformes. Taxonomy. Morphology. Outer Carpathians.**

INTRODUCTION

Small perch-like fishes, common in the Oligocene of the Outer Carpathians, have been traditionally assigned to the perciform species *Serranus budensis* (HECKEL, 1856) (see Paucă, 1933; Jonet, 1958; Jerzmańska, 1968; Kotlarczyk *et al.*, 2006). This species has also been reported in the Oligocene of the Caucasus and the Upper Rhine Graben (Danil'chenko, 1960; Pharisat, 1991; Micklich, 1998; Pharisat and Micklich, 1998; Prokofiev, 2009; Bannikov, 2010). Recently, Prokofiev (2009) selected *S. budensis* as the type species of his new genus *Oligoserranoides*. While, Bannikov (2010) placed *S. budensis* in his new genus *Oliganodon*. The species *S. budensis* was formerly assigned to the family Serranidae by Danil'chenko (1960) and Jerzmańska (1968). However, Micklich (1998) indicated that this assignment was incorrect because of the absence of three spines on the opercle of *S. budensis*, a diagnostic character of the Serranidae (Johnson, 1983). Prokofiev (2009) and Bannikov (2010) assigned *S. budensis* (referred in their papers to as *Oligoserranoides budensis* and *Oliganodon budensis*, respectively) to *Percoidei incertae sedis* due to the lack of diagnostic characters of any fossil or extant percoid family, and noting the morphological differences and similarities to some fossil and extant taxa. Prokofiev (2009) indicated the resemblance of *Oligoserranoides* to *Symphysanodon* (family Symphysanodontidae) and compared characters as the length of the snout, presence of scales on the head, presence of the postmaxillary process, number of rays of the anal and the dorsal fin, number of vertebrae, predorsal formula and the number of epuralia. Bannikov (2010) noted the resemblance of *Oliganodon* to *Symphysanodon* and listed differences as the number of rays of the dorsal fin and the number of abdominal vertebrae. In addition, Bannikov (2010) compared *Oliganodon* to the genera *Pinjalo*, *Parapristipomoides*, *Aphareus* (family Lutjanidae) and *Hemilutjanus* (family Serranidae, after Eschmeyer *et al.*, 2017). From the Oligocene of the Caucasus, Danil'chenko (1960) described *Serranus comparabilis*, latterly, Prokofiev (2009) assigned this species to his new genus *Oligoserranoides*, whereas Bannikov (2010) assigned it to his new genus *Oliganodon*. Under the principle of priority of the International Commission on Zoological Nomenclature, ICZN, (1999), the name *Oligoserranoides*, introduced by Prokofiev (2009), is used herein for the species *budensis* and *comparabilis*.

The large and diverse suborder *Percoidei* has been inadequately defined and serves as a repository for representatives of the order Perciformes that cannot be placed under any other suborder (*e.g.* Johnson, 1984). Percoids are diagnosed by a number of plesiomorphic characters. The fossil record of the *Percoidei* is scarce in comparison to their recent high diversity. The earliest percoid species based on articulated skeletons is from the Cretaceous of India and is classified as *Percoidei incertae sedis* (Arratia *et al.*, 2004). In contrast, the Cenozoic record includes many families defined from articulated skeletons (see *e.g.* Blot, 1980; Patterson, 1993; Kotlarczyk *et al.*, 2006; Bannikov, 2010; Carnevale *et al.*, 2014). The Cenozoic record includes many genera assigned to *Percoidei incertae sedis* due to the lack of diagnostic characters of any fossil or extant family (*e.g.* Bannikov, 2010; Carnevale *et al.*, 2014), *i.e.* families are defined by many diagnostic characters, most of which are of soft anatomy, thus, not possible to recognize in fossil specimens and it is not possible to assign such specimens to any family.

Within the Oligocene record of the *Percoidei incertae sedis*, a few species share many similarities with *Ol. budensis*. For instance, *Caucasoserranoides morozkiensis* Prokofiev, 2009, *Oligoserranoides comparabilis* (Danil'chenko, 1960) and *Pirsagatia sytchevskayae* Prokofiev, 2002. These species have been recorded from the Caucasus (Prokofiev, 2002; 2009). *Carpathoserranoides brnoensis* Prokofiev, 2009 and *Carpathoserranoides polonicus* Prokofiev, 2009, known from the Outer Carpathians, are also similar to *Ol. budensis*. Some percoid fishes from the Eocene of Monte Bolca (Italy) share many similarities with *Ol. budensis*. *Goujetia crassispina* (Agassiz, 1839), *Ottaviania mariae* (Sorbini, 1983), *Ott. leptacanthus* (Agassiz, 1839) and *Veranichthys ventralis* (Agassiz, 1839) were assigned to the Lutjanidae by Bannikov and Zorzin (2004) and Bannikov (2006), and *Jimtylerius temnopterus* (Agassiz, 1836) was classified as *Percoidei incertae sedis* by Bannikov and Carnevale (2007).

The aims of this contribution are i) re-study the holotype (Fig. 1A) and fish material from the Outer Carpathians of Poland previously referred to as *Serranus budensis*, ii) study the newly collected specimens of small perch-like fishes (Figs. 1B and 2), iii) redescribe *Oligoserranoides budensis*, iv) compare *Ol. budensis* with some Palaeogene and living fishes, and v) study the palaeobiogeographic distribution of *Ol. budensis* and some others Oligocene percoid fishes in the Paratethys.

MATERIAL AND METHODS

The holotype of *Oligoserranoides budensis* is housed in the Naturhistorishes Museum, Wien. The specimens previously referred to as *Serranus budensis* are from Prof. A. Jerzmańska's collection (University of Wrocław) from the Rogi and Winnica localities, and from collection of University of Warsaw from Rudawka Rymanowska locality. These localities are in the Outer Carpathians, Poland. The new material (housed at the University of Warsaw) comprises specimens collected by us and our collaborators in 1995–2015 in the Babice-Połanki, Dobra Góra, Futoma, Jamna Dolna, Jasienica Rosielna, Rudawka Rymanowska, and Winnica localities, in the Outer Carpathians, Poland.

Specimens from the Outer Carpathians (deposited in the University of Wrocław and University of Warsaw) are from the Menilite Formation (Fm.) (Kotlarczyk, *et al.*, 2006) of the Silesian and Skole units, southern Poland.

In the Rogi (RO$_1$ in Kotlarczyk *et al.*, 2006) and Winnica (W in Kotlarczyk *et al.*, 2006) localities (near Krosno town), the specimens were derived from the upper part of the Menilite Fm. of the Silesian Unit, ichthyofaunal zone IPM2 (Jerzmańska, 1968; Kotlarczyk *et al.,* 2006, pg.: 66, Table 26).

In the Jasienica Rosielna locality (Wasiluk, 2013) near Krosno town, the specimens were recovered in the upper part of the Menilite Fm. of the Silesian Unit, ichthyofaunal zone IPM2.

In the Rudawka Rymanowska locality in area of Sanok town (Bieńkowska, 2004; RR in Kotlarczyk *et al.*, 2006; Bieńkowska-Wasiluk, 2010), in the Silesian Unit, the specimens were from three exposures (RU 01, RU 02, and RU 03, see Bieńkowska, 2004, Fig. 1) of the Tylawa Limestones and the adjacent shales, ichthyofaunal zone

IPM2. Specimens were derived from the middle layers of the Tylawa Limestones (see Ciurej and Haczewski, 2012; their samples of limestones RR 9/06, RR6A-C/06, Fig. 4).

The Jamna Dolna locality, near the city of Przemyśl (Jerzmańska, 1968; Jerzmańska and Kotlarczyk, 1968; J_{AC} and J_{DG} in Kotlarczyk *et al*., 2006) is in the Skole Unit. Specimens come from the Rudawka Tractionite Member, lithological unit F-G (Fig. 2) of Jerzmańska and Kotlarczyk (1968), ichthyofaunal zone IPM2 (Kotlarczyk *et al.,* 2006, pg.: 66, table 26) above ichthyofaunal subzone IPM2-T. SUB. (*Trachinus* event).

The Dobra Góra locality (DG in Kotlarczyk *et al*., 2006), near Sanok town and Babice-Połanki, (BP1 in Kotlarczyk *et al*., 2006) near Przemyśl city represents the Rudawka Tractionite Member of the Skole Unit, ichthyofaunal zone IPM2 (Kotlarczyk *et al.,* 2006, pg.: 66, table 26).

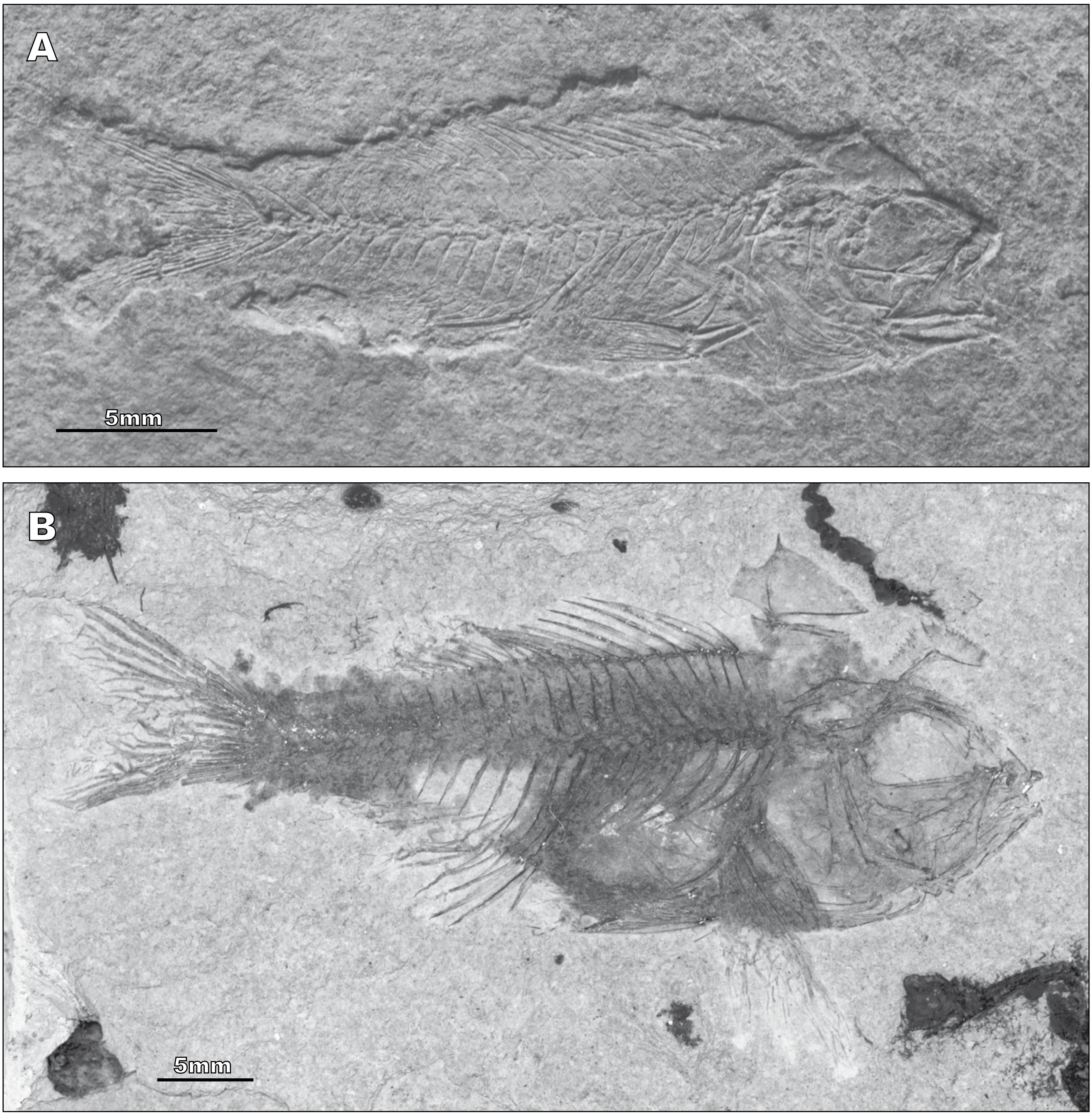

FIGURE 1. *Oligoserranoides budensis* holoypes. A) NHMW 1858/III/25. B) MWGUW ZI/57/014/b.

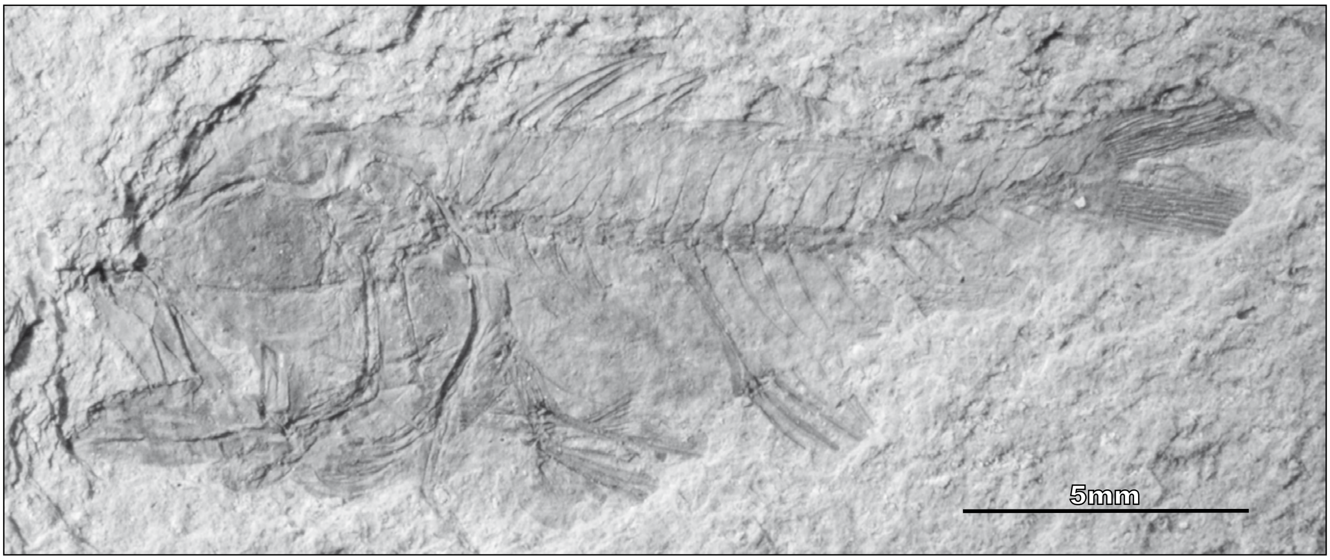

FIGURE 2. *Oligoserranoides budensis.* Juvenile specimen, MWGUW ZI/57/051/b.

In the Futoma (Błażowa) locality near city of Rzeszów (Bąk *et al.*, 2013), in the Skole Unit, the specimens were recovered from the Futoma Diatomite Member, ichthyofaunal zone IPM2.

Summing up, all studied specimens from the Outer Carpathians are Early Oligocene (Rupelian) in age. Ichthyofaunal zone IPM2 is correlated with calcareous nannoplankton Biozone NP23 (see Kotlarczyk *et al.*, 2006). Catalogue numbers of specimens are in Table 1.

Institutional abbreviations: MWGUW, Muzeum Geologiczne im. Stanisława Józefa Thugutta at the Faculty of Geology, University of Warsaw; NHMW, Naturhistorishes Museum, Wien; ZPALWr., Prof. A. Jerzmańska's collection, Department of Palaeozoology, Faculty of Biological Sciences, University of Wrocław.

For the anatomical terminology, we follow Johnson (1981) and Potthoff *et al.* (1988). The anatomical term predorsal formula introduced by Ahlstrom *et al.* (1976, pg.: 297) provides information on the position of the supraneural bones (predorsals) and the anterior dorsal pterygiophores in relation to the anterior neural spines (see Johnson, 1981).

Anatomical abbreviations: aa, angulo-articular; A, anal fin; br, branchiostegal ray; ch, anterior ceratohyal; cl, cleithrum; co, coracoid; cr, crest; D, dorsal fin; d, dentary; ecp, ectopterygoid; eh, epihyal (or posterior ceratohyal); ep, epural; ept, endopterygoid; fr, frontal bone; hh, hypohyal; hp, hypural; hy, hyomandibula; in, interneural space; io, infraorbital; iop, interopercle; l., left; leth, lateral ethmoid; mpt, metapterygoid; mx, maxilla; na, nasal; nsp, neural spine; op, opercle; P, pectoral fin; p, pterygiophore; ph, parhypural; pl, palatine; pmx, premaxilla; pop, preopercle; ps, parasphenoid; pt, posttemporal; pts, pterosphenoid; pu, preural centrum; q, quadrate; ry, ray; ri, rib; r., right; sc, scapula; scl, supracleithrum; SL, standard length; sn, supraneural bone (predorsal); soc, supraoccipital; sp, spine; sy, symplectic; uhy, urohyal; un, uroneural; v, vertebra; vo, vomer; V, pelvic fin.

SYSTEMATIC PALAEONTOLOGY

Order: Perciformes Bleeker, 1859
Suborder: *Percoidei* Bleeker, 1859
Family: *incertae sedis*

GENUS ***Oligoserranoides*** Prokofiev, 2009
Type of species. *Smerdis budensis* Heckel, 1856

Diagnosis (emended). The genus is diagnosed by the following unique combination of characters: maximum body depth in standard length 21-40%; supramaxilla absent; palatine toothless; preopercle with serration; opercle with two spines; 7 branchiostegal rays, ceratohyal without a beryciform foramen; posttemporal with serrated posterior margin; 24 vertebrae (10 abdominal); three predorsals; predorsal formula 0/0/0+2/1+1/ or /0+0/0+2/1+1/; 8 pleural ribs; pectoral fins long, reaching anterior part of anal fin and with 14-17 rays; dorsal fin continuous with 9 to 10 spines and 9 to 11 soft rays; three spines and 8 to 9 soft rays in anal fin; caudal fin forked with 17 principal rays; three epurals; procurrent spur lacking; and ctenoid scales.

Remarks. The two anteriormost neural spines of the holotype are not preserved. Therefore, the predorsal bones are not clearly visible (Fig. 3B). It looks like the predorsal formula could be 0+0+0+2/1+1/, but the two neural spines should be near the supraneural bones. The predorsal formula documented by Prokofiev (2009) is 0/0+0+2/ and /0+0/0+2/. The formula /0+0/0+2+1/1/ for *Oligoserranoides comparabilis* is our interpretation from a figure provided by Bannikov (2010). The first predorsal formula (Fig. 4A) given in the present diagnosis is the most frequent in specimens from the Outer Carpathians. Both patterns of predorsal formulae (0/0/0+2/1+1/ and /0+0/0+2/1+1/) occur in specimens from the same locality (*e.g.* Jamna Dolna, Jasienica Rosielna, Rogi, Rudawka Rymanowska). We have observed other patterns, such as the first given by Prokofiev and with variation of the position of two anterior neural spines on some specimens with signs of slight postmortem displacement of some head bones or in which one of the anterior neural spines not visible.

Oligoserranoides budensis (Heckel, 1856) Figures 1-6

1856. *Smerdis budensis* Heckel, pg.: 264, pl. XI, Fig. 16.
1960. *Serranus budensis* Danil'chenko, pg.: 101, Fig. 21; pl. XXV, Fig. 4.
1968. *Serranus budensis* Jerzmańska, pg.: 449, Fig. 19; pl. VI, Fig. 3.
2009. *Oligoserranoides budensis* Prokofiev, pg.: 205, Figs. 5-7 and 9.
2010. *Oliganodon budensis* Bannikov, pg.: 86, pl. VII, Figs. 2 and 3.
2016. *Oliganodon budensis* Přikryl *et al.*, pg.: 37, Fig. 4E.

Holotype. NHMW 1858/III/25.

Type locality and age. Blocksberg near Ofen, currently Budapest (Schultz, 2013), Hungary; Oligocene.

Diagnosis. As for genus.

Material. MWGUW (46 individuals); ZPALWr. (33 individuals); for catalogue numbers of specimens see Table 1.

Measurements. See Table 2.

Description

Skull

The skull bones of the holotype are poorly preserved, with most of the bone margins unrecognizable (Fig. 3A; B). The opercular bones and jaws are moderately preserved. Most of the anatomical details were observed on specimens MWGUW ZI/57/015, MWGUW ZI/57/028 (Fig. 3E; F), MWGUW ZI/57/036, MWGUW ZI/57/046 (Fig. 3C; D), ZPALWr. A/920, ZPALWr. A/922. The head length is 33 to 42% SL. The frontal bones are smooth, without well-developed crests. The limits of the skull roof bones and the position of the sensory canals are unclear. The parietal bones seem to be about two times smaller than the frontals. The supraoccipital crest is present but not well developed; specimen MWGUW ZI/57/046 has a serration preserved on its posterior margin (Fig. 3C; D). Anteriorly, the frontal sutures with the ethmoid region, but the limits of the nasal bone and lateral ethmoid cannot be determined. A narrow nasal bone is probably preserved in MWGUW ZI/57/046. Lateroanteriorly, a large element, which we interpret as the lateral ethmoid, is present. The horizontal diameter of the orbit is 23 to 45% of the head length. The posterior, anterior and ventral limits of the orbit are usually unclear. The parasphenoid is usually observed below the middle region of the orbit, about the lower third of the orbit.

TABLE 1. Studied specimens from the Outer Carpathians and its localities

Rogi	ZPALWr. A/920-–923, A/925, A/1260, A/1262, A/1270–1272, A/1289–1290, A/1292, A/1294–1295, A/1308, A/1392, A/1437, A/1442–1443
Winnica	ZPALWr. A/1467, A/1471, A/1474, A/1476–1477, A/1480, A/1483, A/1485, A/1487, A/1494, A/1507, A/1509–1510; MWGUW ZI/57/029
Jasienica Rosielna	MWGUW ZI/57/016, ZI/57/035, ZI/57/039–41
Rudawka Rymanowska	MWGUW ZI/57/018–20, ZI/57/022, ZI/57/028, ZI/57/033–34, ZI/57/042, ZI/57/047, ZI/57/053–55, ZI/57/057–60, ZI/57/063–64, ZI/57/090, ZI/57/103, ZI/57/108–109, ZI/57/110/1
Jamna Dolna	MWGUW ZI/57/014–15, ZI/57/036, ZI/57/046, ZI/57/048, ZI/57/050–51, ZI/57/104–107
Dobra Góra	MWGUW ZI/57/065–67
Babice-Połanki	MWGUW ZI/57/044
Futoma	MWGUW ZI/57/023

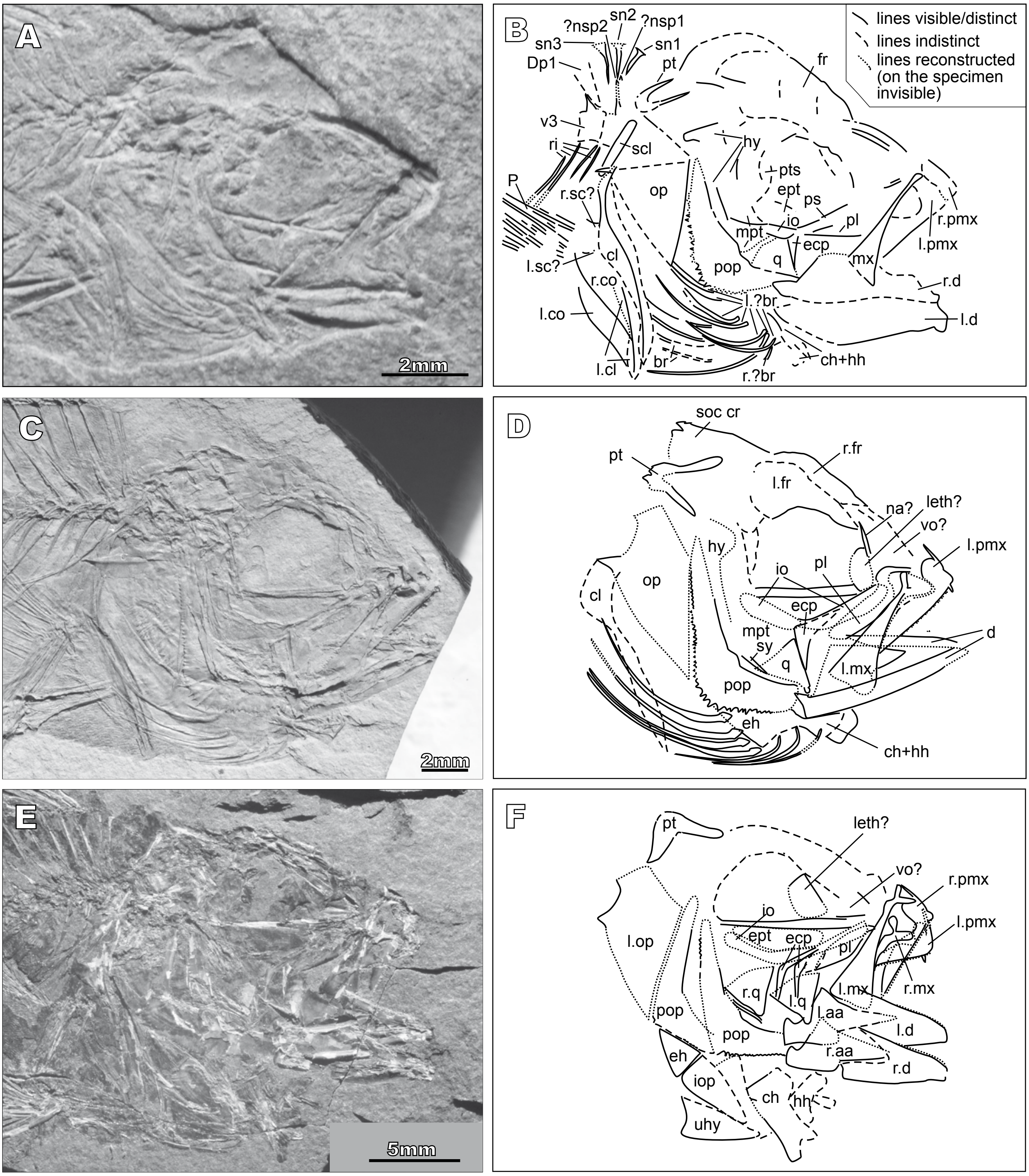

FIGURE 3. Skull of *Oligoserranoides budensis.* A, B) holotype, NHMW 1858/III/25 photo (A) and camera lucida drawing (B). C, D) MWGUW ZI/57/046 photo (C), specimen is preserved as an imprint of bones (concave), photo made in a special technique to show a convex specimen, as if the bones were preserved, (D) interpretative drawing. E, F) MWGUW ZI/57/028/a photo (E) and drawing (F). Abbreviations: br, branchiostegal ray; ch, anterior ceratohyal; ch+hh, anterior ceratohyal plus hypohyal; cl, cleithrum; co, coracoid; d, dentary; Dp, dorsal pterygiophore; ecp, ectopterygoid; eh, epihyal; ept, endopterygoid; fr, frontal bone; hh, hypohyal; hy, hyomandibula; io, infraorbital; iop, interopercle; l.aa, left angulo-articular; l.br, left branchiostegal ray; l.cl, left cleithrum; l.co, left coracoid; l.d, left dentary; l.fr, left frontal; l.mx, left maxilla; l.pmx, left premaxilla; l.q, left quadrate; l.sc, left scapula; leth, lateral ethmoid; mpt, metapterygoid; mx, maxilla; na, nasal; nsp, neural spine; op, opercle; P, pectoral fin; pl, palatine; pop, preopercle; pt, posttemporal; pts, pterosphenoid; q, quadrate; r.aa, right angulo-articular; r.br, right branchiostegal ray; r.co, right coracoid; r.d, right dentary; r.fr, right frontal bone; r.pmx, right premaxilla; r.q, right quadrate; r.sc, right scapula; ri, rib; scl, supracleithrum; sn, supraneural bone (predorsal); soc cr, supraoccipital crest; sy, symplectic; uhy, urohyal; v, vertebra; vo, vomer.

The infraorbital bones are usually no visible or not preserved. Probably, they were thin and small. The lacrimal seems to be the largest infraorbital, but its shape is unknown. Fragments of possible infraorbitals 2 or 3 are preserved.

The hyomandibula lies vertically to the body axis. The symplectic seems to be slim. The metapterygoid is only partially visible. The endopterygoid is large. The quadrate is triangular and meets anteriorly with the thin ectopterygoid, which does not project posteriorly to articulate with the metapterygoid (see Johnson, 1981, figs. 21 and 22). Posterodorsal or posteroventral process of the quadrate is not visible. The ectopterygoid articulates anteriorly with the long and thin palatine. Teeth or sockets for teeth on the endopterygoid, ectopterygoid and palatine have not been observed.

The opercle has two small spines (Fig. 4B) and is much taller than wide. The limits of the subopercle are not visible. The interopercle is triangular, well developed, and with a straight postero-dorsal border. The preopercle has a serration on both the posterior and ventral margins (Fig. 4C; D). Small specimens have a serration and a few distinct spines where posterior and ventral margins meet (see Jerzmańska, 1968, fig. 19A; B). In larger specimens, serrations are slightly larger and more distantly placed at the margin where the posterior and ventral margins meet. Specimen MWGUW ZI/57/046 (41.6 SL) has about 44 preopercular spines in serration. Dorsal and ventral, *i.e.* horizontal axes of the preopercle form an angle of slightly more than 90˚.

The hyoid arch is partially preserved. The epihyal (or posterior ceratohyal) is triangular. The ceratohyal (or anterior ceratohyal) does not present a beryciform foramen. The number of branchiostegal rays in the holotype is unclear, 6 or 7 rays are preserved. Specimens MWGUW ZI/57/015, MWGUW ZI/57/036, MWGUW ZI/57/046 have 7 branchiostegal rays. The number of branchiostegal rays on anterior and posterior ceratohyals and epihyal is unclear. The anterior three rays are thinner

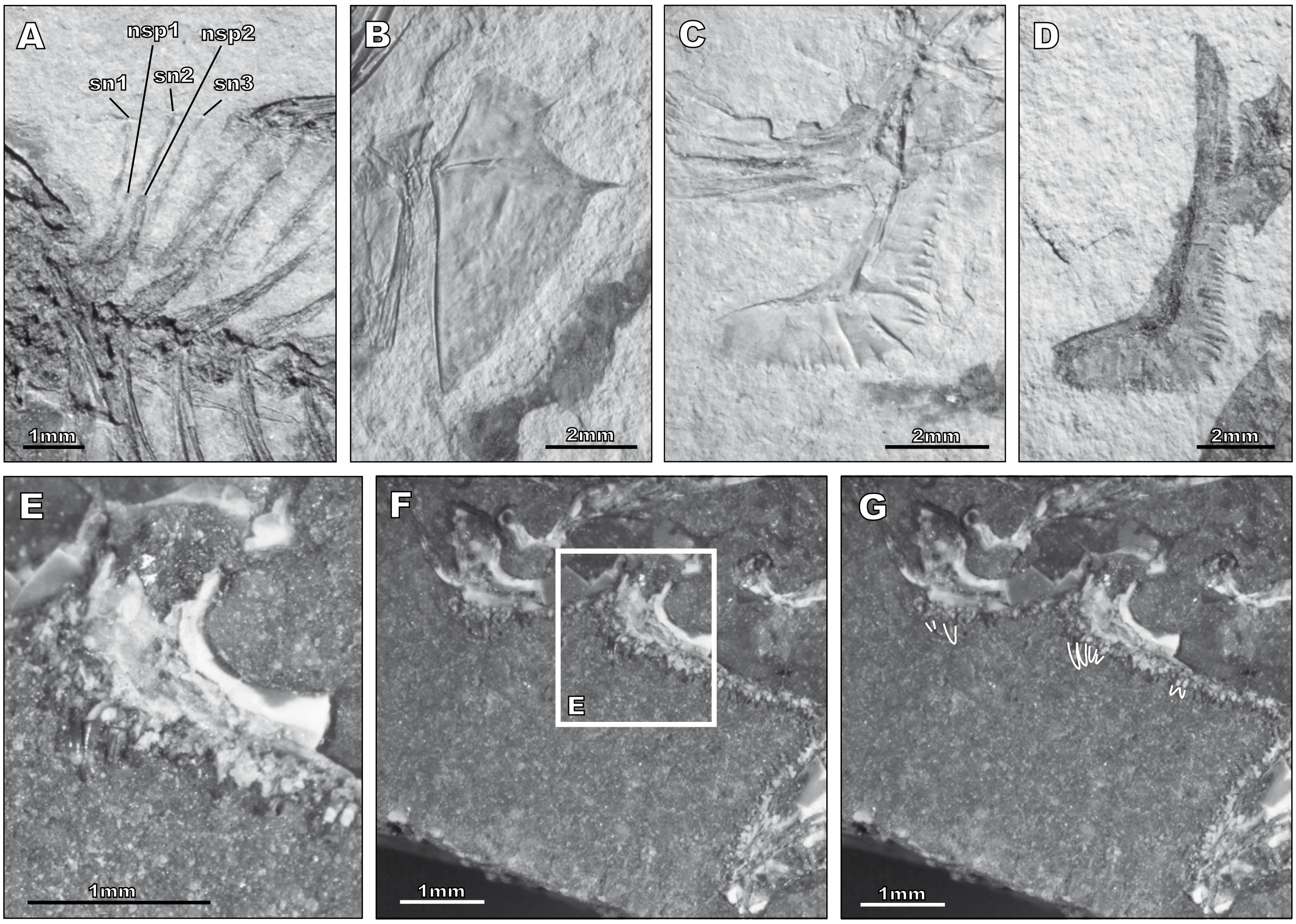

FIGURE 4. Details of the skull and anterior vertebrae of *Oligoserranoides budensis.* A) anterior neural spines (nsp) associated with supraneural bones (sn), MWGUW ZI/57/065. B) opercle MWGUW ZI/57/014/b. C) preopercle MWGUW ZI/57/014/b. D) preopercle MWGUW ZI/57/029. E) premaxilla MWGUW ZI/57/033/a. F–G) jaws MWGUW ZI/57/033/a; area visible on E is indicated on F; G with outline of well-preserved teeth.

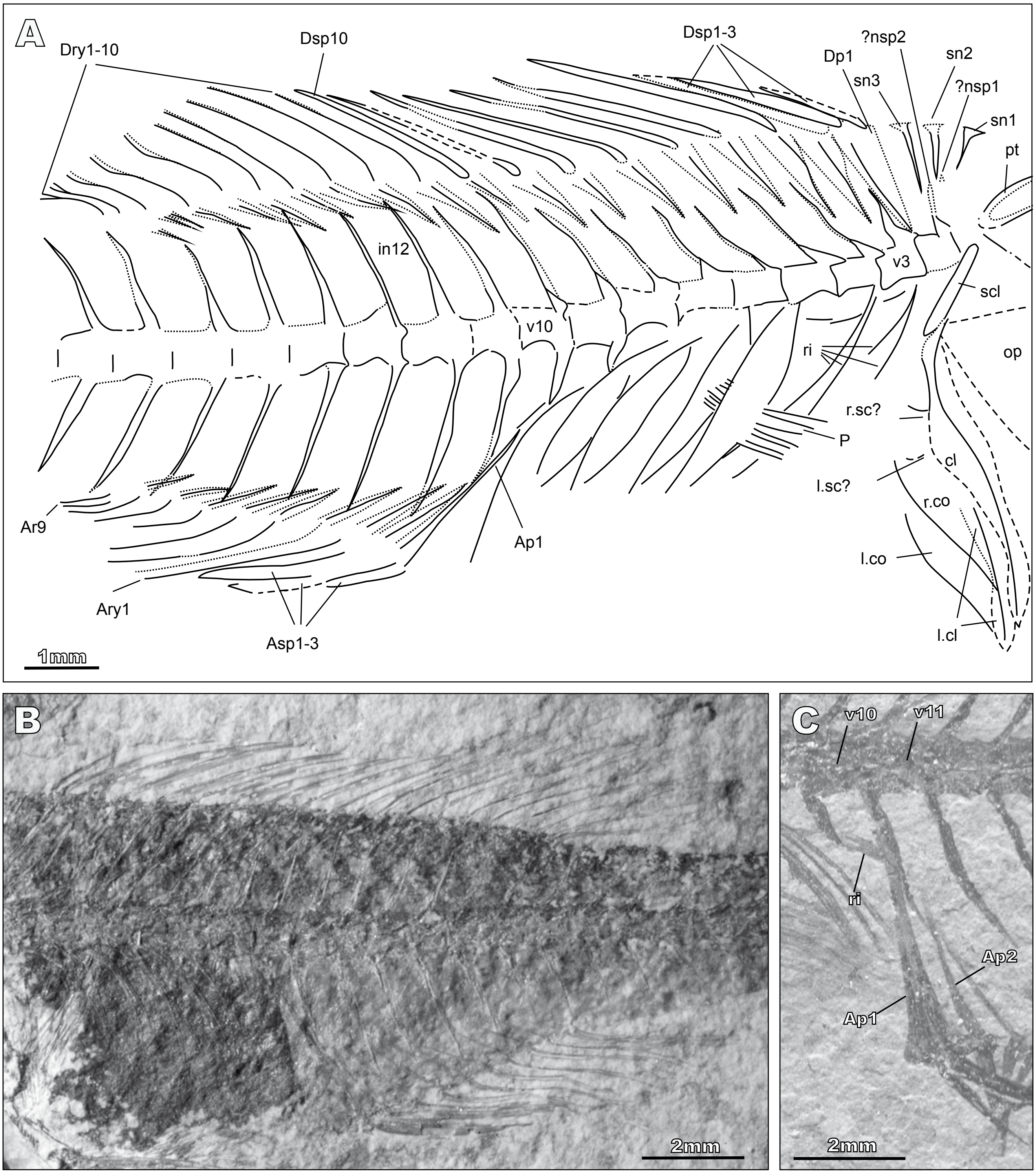

FIGURE 5. Details of vertebral column, dorsal and anal fins of *Oligoserranoides budensis*. A) Camera lucida drawing of holotype, NHMW 1858/III/25, for interpretation of lines see Fig. 3B. B) Dorsal and anal fin MWGUW ZI/57/058 C) Anterior caudal region and anterior part of anal fin, ZPALWr. A/1494. Abbreviations: Ap, anal pterygiophore; Ary, anal ray; Asp, anal spine; cl, cleithrum; Dry, dorsal ray; Dsp, dorsal spine; in, interneural space; l.cl, left cleithrum; l.co, left coracoid; l.sc, left scapula; nsp, neural spine; op, opercle; P, pectoral fin; pt, posttemporal; r.co, right coracoid; r.sc, right scapula; ri, rib; scl, supracleithrum; sn, supraneural bone (predorsal); v, vertebra.

than the posterior ones. The urohyal is triangular. Remains of ceratobranchials and epibranchials are preserved but their reconstruction was impossible. Long gill rakers were observed.

The mouth is terminal, the snout length is usually smaller than the horizontal diameter of the orbit. The premaxilla has well developed ascending and articular processes. The ascending process is sharp and narrow, slightly higher than the articular process, which is rounded, not fused along its anterior border with the ascending process. The postmaxillary process is broadly based, not finger-like. The premaxilla usually bears small conical teeth, but some specimens have the teeth considerably enlarged anteriorly (Figs 3D, F; and 4E, G), other specimens seem to be toothless. Because of a poor state of preservation, the teeth are not visible in the jaws of the holotype. The toothless maxilla is triangular, its depth increases posteriorly. The supramaxilla is absent.

The lower jaw is moderately long and deep, and bears small teeth. The jaw articulation lies below the middle of the orbit or slightly posteriorly (Fig. 3). The dentary is a "V" shaped bone with an angle of "V" forming the symphyseal region. The angulo-articular is about the same size as the dentary. The limits of the angulo-articular and the retroarticular are not visible. The pores of the mandibular sensory canal are not well preserved.

Vertebral column, ribs and intermuscular bones

There are 24 vertebrae (including the preural centrum 1), 14 of which are caudal. In the holotype, the first vertebra is not preserved, but the tips of the first and second neural spines seem to be visible (Figs. 3B and 5A). The neural spines of abdominal centra 3–4 (Fig. 4A) are broader than the remaining spines. The neural spines of centra 9–11 are the tallest. Neural prezygapophyses are visible on centra 5–24 (specimen MWGUW ZI/57/046). The presence of neural postzygapophyses, haemal prezygapophyses and postzygapophyses is unclear. We have observed parapophyses on centra 6–10 (specimen MWGUW ZI/57/046); the posterior ones are the largest. The first caudal vertebra has a long hemal spine (Fig. 5A; C). The hemal spines of preural centra 2–3 are thicker than the anterior ones and probably autogenous (specimen MWGUW ZI/57/028). The neural spine of preural centrum 3 is longer and thicker than the anterior ones.

Eight pairs of pleural ribs are articulated with vertebrae 3–10. On the holotype, the last pair is difficult to recognize.

Some thin epipleurals are visible, but their number is unclear. Specimen MWGUW ZI/57/014, probably has 5 pairs of epipleurals associated with vertebrae 1–5. Intermuscular bones are absent in the caudal region. Three predorsal bones (supraneurals) are present. The first predorsal is usually anterior or posterior to the first neural spine. The second predorsal is between the first and second neural spine. The third predorsal is posterior to the second neural spine.

Pectoral girdle and fin

The post-temporal has a serrated posterior margin (see Fig. 3D; Prokofiev, 2009, fig. 7). Its intercalar process is slightly shorter than dorsal process for contacting the epiotic. The supracleithrum is elongate and slim, its ventral portion overlaps the dorsal tip of the cleithrum (Figs. 3A and 5A). The cleithrum is slightly S-shaped. It has a broad triangular-shaped shelf (posterior process) dorsally and a broad shelf area ventrally. The ventral part ends sharply. The postcleithrum is a well-developed, large and broad bone with its ventral tip near the ventral margin of the body. The boundary between postcleithra 1 and 2 is unclear. The small scapula has a foramen (specimen MWGUW

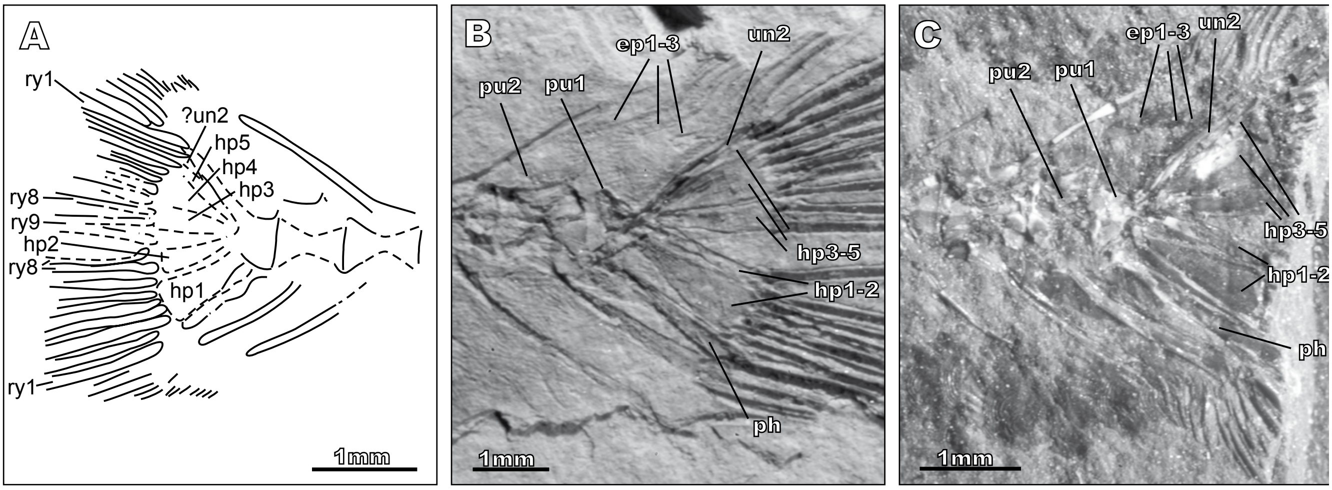

FIGURE 6. Details of caudal endoskeleton and fin of *Oligoserranoides budensis*. A) Camera lucida drawing of holotype, NHMW 1858/III/25. B) MWGUW ZI/57/016/a. C) MWGUW ZI/57/090/a. Abbreviations: ep, epural; hp, hypural; ph, parhypural; pu, preural centrum; ry, ray; un, uroneural.

TABLE 2. Morphometric measurements of the studied specimens of *Oligoserranoides budensis,* and from Danil'chenko (1960), Jerzmańska (1968) and Bannikov (2010)

	Holotype NHMW 1858/III/25	specimens MWGUW	specimens ZPALWr.	Danil'chenko (1960)	Jerzmańska (1968)	Bannikov (2010)
SL (mm)	25.3 *24	18.7-50.6	13-53	40-70	15.5-77	—
Maximum body depth in SL (%)	27.7 *33.3	22-40	21-33	28-31	25-39.8	27-33
Head length in SL (%)	33.6 *33.3	31-43	34-38	33-35	—	33-36
Horizontal diameter of orbit in head length (%)	23.5 *25	23-45	29-35	—	—	—

* estimated if specimen was preserved with jaws closed

ZI/57/015). The coracoid is large, broad and deep, but it appears to be a thin bone. There are four small proximal radials (specimen MWGUW ZI/57/015).

The pectoral fins attach relatively low on the flank, about the lower third of the body depth. They bear 15–20 rays each, which are long and reach the anterior-middle part of the anal fin (hemal spine of fourth caudal vertebra). The length of those fins cannot be established in the holotype and the number of rays is unknown.

Pelvic girdle and fin

The pelvic fins attach to the body just below the pectoral fins or slightly posteriorly. They bear one spine and five rays each. Two elongate, triangular-shaped basipterygia (pelvic plates) are sutured to each other medially. The subpelvic and postpelvic processes are developed but their shapes are unclear. The presence of accessory subpelvic keel is unclear; most probably it is absent.

Dorsal fin

The dorsal fin is rather small, and bears 10 spines and 10 soft rays in the holotype (Fig. 5A) and in most of the studied specimens. There is a variability in the number of rays in the dorsal fin bearing 9 to 11 soft rays and sometimes 9 spines. The fin is continuous, with the spinous part not separated by a notch from the soft part. The posterior part of the fin (with soft rays) is usually slightly higher than the spinous one (Fig. 5B). The first dorsal pterygiophore or proximal radial 1 (Figs. 4A and 5A) is placed in the third interneural space (the first interneural space is between the skull and the first neural spine) and bears two first spines in a supernumerary association and the third one in a serial association. The second and third pterygiophore are placed together in the fourth interneural space. Pterygiophores 4–10 are placed respectively in the succeeding interneural spaces. Two pterygiophores are placed in interneural spaces 12 and 14, and one pterygiophore is in interneural space 13. The remaining posterior pterygiophores are poorly preserved and often they are displaced. The presence of three segmental pterygiophores is unclear.

Anal fin

The anal fin bears three spines and 8 to 9 soft rays (9 in the holotype, Fig. 4A). The first spine is the shortest, the third spine is the longest.

The first anal pterygiophore is enlarged and positioned more or less anteriorly to the hemal spine of the first caudal vertebra (Fig. 5A; C). Its triangular shape is unclear in the holotype due to its poor preservation, because it is not in lateral view but is slightly rotated. The dorsal tip of this pterygiophore often reaches the hemal arch of the last abdominal vertebra. Two supernumerary spines and one serially associated spine are present on the first anal pterygiophore. The presence of three segmental pterygiophores is unclear.

Caudal skeleton and fin

The caudal fin consists of 17 principal rays (one unbranched, 7 branched in the lower lobe, 8 branched in the upper lobe and one unbranched). About 10 dorsal and ventral procurrent rays are present. The caudal skeleton is represented by five hypurals, one parhypural and three epurals (in the holotype the epurals are not preserved and the hypurals are poorly preserved; see Fig. 6). Details of the first uroneural (the so-called stegural) and second uroneural are not visible. Hypurals are distributed in two groups (1+2; 3+4+5), which are separated by the hypural diastema. The neural spine of the second preural centrum is short. Neural spine of third, and hemal spines of second and third preural centra participate in the support of the principal and procurrent caudal rays. The parhypural is as broad as the hemal spine of the second preural centrum. Epurals are narrow and usually difficult to notice. A procurrent spur has not been observed in the holotype or in the additional material.

Scales

Scales are ctenoid, moderate in size, with ctenii at their posterior margins and a few radii (up to 12) in the anterior fields. Ctenoid scales are observed on the trunk and cheek (anteriorly to the preopercle, below the orbit, posteriorly to the region occupied internally by the ectopterygoid; specimens MWGUW ZI/57/014, MWGUW ZI/57/028, MWGUW ZI/57/036, MWGUW ZI/57/046). Ctenoid scales seem to be present on the opercle (specimen MWGUW ZI/57/046).

The lateral line is enclosed by scales. It is continuous, concurrent with the dorsal profile, and descends to the level of the vertebral column near the twentieth vertebra (unclear in the holotype).

Pigmentation

Black and brown pigmentation appears on the dorsal part of the body (Fig. 5B; see Bieńkowska, 2004, fig. 16; Prokofiev, 2009). Series of small melanophores are concentrated near the dorsal margin and disappear gradually near the body midline.

REMARKS

Prokofiev (2009) illustrated the first pterygiophore of the anal fin positioned posteriorly to the hemal spine of the first caudal vertebra. In the holotype of *Ol. budensis* and in the studied Carpathian material, the first pterygiophore of the anal fin is positioned anteriorly to the hemal spine of the first caudal vertebra (Fig. 5A; C).

Only small teeth were mentioned in previous studies of *Ol. budensis* (see Danil'tshenko, 1960; Jerzmańska, 1968; Prokofiev, 2009; Bannikov, 2010). In the studied material, many specimens are preserved as imprints of bones. In such mode of preservation, the observation of teeth was difficult. Sometimes the teeth seem to be small, but on the counterpart enlarged teeth are distinct. In the ZPALWr. collection of *Ol. budensis*. from Rogi and Winnica, both small teeth and enlarged teeth were observed. Přikryl *et al.* (2016) noted slightly enlarged teeth around the premaxillary symphysis (they ascribed their material to *Oliganodon budensis*).

Specimens ZPALWr. A/1266, A/1274, A/1350-1351, A/1359, A/1369, A/1375, A/1380, A/1386, A/1436, A/1440-1441, A/1458, A/1468-1470, A/1473, A/1475, A/1482, A/1486, A/1488 assigned by Jerzmańska (1968) to *Serranus budensis* probably belong to *Ol. budensis* according to our studies. However, they are too fragmentary or poorly preserved to justify their taxonomic assignment to *Ol. budensis*. In our opinion, the above listed specimens should be classified as *Percoidei incertae sedis*.

In this contribution, we have re-studied several specimens published previously as Serranidae by Bieńkowska (2004, *e.g.* fig. 16) and Bieńkowska-Wasiluk (2010, *e.g.* fig. 28A, fig. 32 specimen a). According to our present observations, some of those previously published specimens belong to *Ol. budensis* (specimens MWGUW ZI/57/018, ZI/57/028, ZI/57/033, ZI/57/034/1, ZI/57/042, ZI/57/047, ZI/57/053-64, ZI/57/090, ZI/57/103, ZI/57/109, ZI/57/110/1), others should be assigned to *Percoidei incertae sedis* (specimens MWGUW ZI/57/017, ZI/57/021, ZI/57/032, ZI/57/037-38, ZI/57/043, ZI/57/045/1-2, ZI/57/056, ZI/57/061-62) due to the lack of diagnostic features, although they have an overall similarity to *Ol. budensis*, whereas the remaining specimens are in need of revision and are not discussed here.

DISCUSSION

The small percoid fishes *Caucasoserranoides morozkiensis*, *Carpathoserranoides brnoensis*, *Carpathoserranoides polonicus*, *Oligoserranoides budensis*, *Ol. comparabilis* and *Pirsagatia sytchevskayae* from the Oligocene of the Paratethys have been described by Danil'chenko (1960), Prokofiev (2002, 2009) and Bannikov (2010).

The measured range in the body proportions of *Ol. budensis*, *i.e.* maximum body depth in standard length, is wide and acquires 21–40%. This overlaps with the variability of *Ol. comparabilis*, *i.e.* 34–37% (Table 3). The range of this morphometric ratio for *Ol. budensis* according to Bannikov (2010) is 27–33%. According to Danil'chenko (1960), *Ol. comparabilis* differs from *Ol. budensis* by a longer head, larger maximum body depth and more anterior origin of the dorsal fin. According to Bannikov (2010), in the dorsal fin *Ol. comparabilis* has 9 soft rays and *Ol. budensis* has 10 soft rays. Among the studied specimens, there are individuals with 9 soft rays, there is no gap in the maximum body depth in standard length at 33–34% (Fig. 7). It is possible that *Ol. budensis* as we defined it herein includes also *Ol. comparabilis*, but further studies of specimens of the latter species are necessary for resolving this issue. In the current interpretation, there is no difference between the species *Ol. budensis* and *Ol. comparabilis*.

Oligoserranoides budensis shares many osteological and meristic characters as well as measurements with the Oligocene representatives of *Carpathoserranoides* and *Caucasoserranoides*. *Carpathoserranoides* differs from *Oligoserranoides* in having 9 (*versus* 10) abdominal vertebrae. *Caucasoserranoides* differs from *Oligoserranoides* in the predorsal formula (Table 3). However, the variability in the predorsal formula may not be of taxonomic significance (see Ahlstrom *et al.*, 1976) as it is assumed for *Ol. budensis*. Further studies are necessary in order to recognise, whether *Carpathoserranoides*, *Caucasoserranoides* and *Oligoserranoides* are closely related or even conspecific.

Oligoserranoides budensis differs from *Pirsagatia sytchevskayae* in the predorsal formula, the number of branchiostegal rays, number of abdominal/caudal vertebrae (Table 3), and posteriorly inclined neural spines of the vertebrae (*vs.* neural spines in the middle part of the vertebral column, nearly vertically oriented).

Prokofiev (2009) noticed the differences between *Ol. budensis* and other perciforms such as *Dapalis*, *Dapaloides* and *Properca* from the Oligocene of western Europe and *Bilinia* from the Oligocene-Miocene of the Czech Republic. Although *Ol. budensis* is defined in this paper in a few characters that are different than those suggested by Prokofiev (2009), the differences presented by Prokofiev (2009) between *Ol. budensis* and *Dapalis*, *Dapaloides*, *Properca* and *Bilinia* are significant.

With *Jimtylerius temnopterus* from the Eocene of Monte Bolca (Italy), *Ol. budensis* shares the predorsal formula, the number of dorsal and caudal fin rays, number of anal fin spines, number of vertebrae and body proportions (Table 3) (see Bannikov and Carnevale, 2007). *Ol. budensis* differs from *J. temnopterus* in the presence of ctenoidal scales, enlarged anterior teeth, and absence of a procurrent spur. In both species, the hypurals are in two groups (1+2, 3+4+5) separated by a diastema, the neural and haemal spines of the third preural vertebra are long, the neural spine of the second preural vertebra is reduced to a short crest, and there are three epurals. *J. temnopterus* was classified as *Percoidei incertae sedis* by Bannikov and Carnevale (2007).

Oligoserranoides budensis is similar to *Ottaviania mariae*, assigned by Bannikov and Zorzin (2004) to the Lutjanidae and to *Ott. leptacanthus* (Table 3). Both species are from the Eocene of Monte Bolca. *Ott. mariae* resembles *Ol. budensis* in the body proportions, number of rays in dorsal and anal fins, and presence of ctenoidal scales. It differs in the predorsal formula, presence of large conical teeth, fusion of hypurals 1–2 and 3–4, and presence of a broadly flanged last pleural rib. *Ott. leptacanthus* (see Bannikov, 2006) differs from *Ol. budensis* in the number of abdominal vertebrae (but this character needs verification and could be the result of postmortem processes), presence of cycloid scales, and fusion of hypurals 1–2 and 3–4. Two species *Goujetia crassispina* and *Veranichthys ventralis* from the Eocene of Monte Bolca assigned to the Lutjanidae (Bannikov, 2006) significantly differ from *Ol. budensis*. The dorsal profile of the body being more convex than ventral and the conical teeth distinguish both genera from *Ol. budensis*. Both genera share the number of vertebrae and number of dorsal fin rays with *Ol. budensis*. *Goujetia, Jimtylerius, Ottaviania* and *Veranichthys* were described based on a very limited number of individuals that were much larger than *Ol. budensis*, which limits the possibility of comparison.

Oligoserranoides budensis is similar to family "Serranidae" *Percoidei incertae sedis* from the Palaeocene of Mexico (see Alvarado-Ortega *et al.,* 2015) in the predorsal formula, number of spines and soft rays of the dorsal fin, number of vertebrae, number of spines in the anal fin, and presence of ctenoidal scales. It differs, however, in the number of soft rays in the anal fin (8–9 *vs.* 7) and in the absence of the supramaxilla.

Oligoserranoides budensis is similar in some characters to *Proserranus lundensis* (Davis, 1890), a putative perciform, from the Palaeocene (Danian) sediments of Limhamn, southern Sweden (Patterson, 1964). *Ol. budensis* shares with the latter species the number of vertebrae, anal spines, dorsal spines and soft rays, and the presence of ctenoidal scales. The differences include a toothless palatine and serration on the posttemporal posterior margin in *Ol. budensis*. The lack of many anatomical data for *Proserranus* does not allow for a more detailed comparison of the species.

The presence of spines in the dorsal and anal fins, one spine and five rays (I, 5) in the pelvic fin, 17 principal (I, 8, 7, I) rays in the caudal fin arranged on five hypurals and the parhypural, 7 branchiostegal rays and absence of the second ural centrum indicate alignment of *Ol. budensis* with perciform fishes (see Johnson and Patterson, 1993). The number of rays in the pelvic and caudal fins is a primitive perciform character (Johnson, 1984). *Ol. budensis* presents the characteristics of Percoidei (see Johnson, 1984). The presence of three predorsal bones, the predorsal formula

TABLE 3. Comparison of some osteological characters and measurements of *Oligoserranoides budensis* and of some Palaeogene and extant fishes

	Number of vertebrae (number of abdominal + caudal vertebrae)	Anal fin	Dorsal fin	Predorsal formula	Enlarged anterior teeth	Head length in standard length	Body depth in standard length	Age
Oligoserranoides budensis **this study**	24 (10+14)	III + 8-9	IX-X+9-11	0/0/0+2/1+1/ and /0+0/0+2/1+1/	Yes and no	31-43%	21-40%	Oligocene
Oligoserranoides comparabilis acc. to Bannikov (2010)	24 (10+14)	III+8[*1]	X+9[*1]	/0+0/0+2+1/1/[*2]	No	32-37%	34-37%	Oligocene
Caucasoserranoides morozkiensis acc. to Prokofiev (2009)	24 (10+14)	III+8-9	X+10	0/0+0+2/1+1/1/ and 0/0+0+2/1/1/[*3]	Yes	36.4-39.4%	26.7-27.3%	Oligocene
Carpathoserranoides brnoensis acc. to Prokofiev (2009)	24(9+15)	III+9	X+10	0+0+0/2/1 and /0+0+0/2/1/	No	*ca.* 34% (2.9 times in SL)	42%	Oligocene
Carpathoserranoides polonicus acc. to Prokofiev (2009)	24(9+15)[*4]	III +*ca.* 8	X+10?	/0+0+0/2+1/1[*5]	No	*ca.* 37% (2.7 times in SL)	-	Oligocene
Pirsagatia sytchevskayae acc. to Prokofiev (2002)	25(11+14)	III + 9	IX + 10	0/0+0/2/1	No	36.4%	33.3%	Oligocene - Lower Miocene
Jimtylerius temnopterus acc. to Bannikov and Carnevale (2007)	24(10+14)	III+7	X+9	/0+0/0+2/1+1/	No	31%	31%	Eocene
Ottaviania mariae acc. to Bannikov and Zorzin (2004)	24(10+14)	III+8	X+11	/0+0+0/2/1+1/	Yes	34%	30%	Eocene
Ottaviania leptacanthus acc. to Bannikov (2006)	24(11+13)	III+8	X+11	-	-	33%	30%	Eocene
Symphysanodon acc. to Anderson (1970); Johnson (1984)	25(10+15)	III+7-8	IX + 10	0/0/0+2+1/1/1/ and 0/0/0+2/1+1/1/	Yes	27-36%	20-36%	extant
Lutjanus cyanopterus acc. to McEachran and Fechhelm (2005); Fahay (2007)	24(10+14)	III+7-8	X+14	0/0/0+2/1+1/	Yes	36-37%	29-32%	extant
Ocyurus chrysurus acc. to Allen (1985); McEachran and Fechhelm (2005); Fahay (2007)	24(10+14)	III+8-9	IX–XI +12–14	0/0/0+2/1+1/	Yes	*ca.* 29%	30-34%	extant

[*1] According to Danil′chenko (1960) for *Serranus comparabilis.*
[*2] From fig. 45 of Bannikov (2010).
[*3] The first predorsal formula is from the text and the second from fig. 1 of Prokofiev (2009).
[*4] In the text (Prokofiev, 2009) 9+15=25 vertebrae are cited, whereas 24 vertebrae are mentioned for the genus.
[*5] From fig. 15 of Prokofiev (2009).

0/0/0+2/, 24 vertebrae, three anal spines, the presence of five hypurals, three epurals, one ural centrum, and a low neural crest on the second preural centrum of *Ol. budensis* are primitive features of the Percoidei (see Johnson, 1984). The predorsal formula /0+0/0+2/1+1/ is a derived character and is present in the Acropomatidae, which, however, differ in the presence of two dorsal fins (see Johnson, 1984; Fahay, 2007).

Bannikov (2010) indicated the similarity between *Ol. budensis* and some genera of the family Lutjanidae (*Pinjalo*, *Parapristipomoides*, *Aphareus*) and *Hemilutjanus* (Serranidae). *Ol. budensis* shares with Lutjanoidea many characters, such as, ctenoid scales, scales on cheek, a complete lateral line, the number of dorsal and anal fin spines and soft rays, a single dorsal fin, the number of rays in caudal, pectoral and pelvic fins, a serrated preopercle, an opercle with two spines, a serrate posterior margin of the posttemporal, a premaxilla with larger conical teeth, the supramaxillary bone being absent, a ectopterygoid without teeth, the general anatomy of the suspensorium, and the number of branchiostegals, vertebrae and pleural ribs, three predorsals and the predorsal formula, the procurrent spur being absent, three epurals, and the number

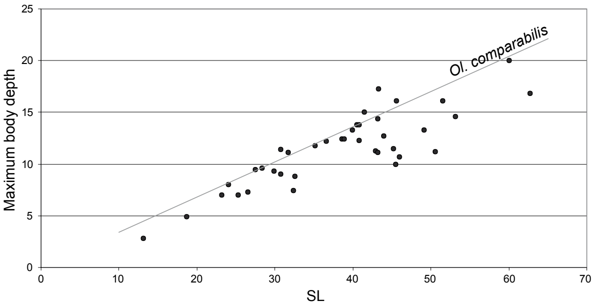

FIGURE 7. Measurements variability of *Oligoserranoides budensis*, maximum body depth and standard length. The line indicates 34% maximum body depth in standard length for *Ol. comparabilis*.

of hypurals (see Johnson, 1981). *Ol. budensis* differs from the superfamily Lutjanoidea in having a toothless palatine. Maybe *Ol. budensis* is a member of the superfamily Lutjanoidea, but further detailed studies of the osteology of the species and the representatives of the superfamily (both fossil and extant) are necessary.

Further research is necessary especially for the observation of characters typical for the Lutjanoidea such as presence of trisegmental posterior 1-7 dorsal and anal pterygiophores, the shape of the lacrimal, presence of the subocular shelf, presence of well-developed metapterygoid lamina, details of the suspensorium, inserting of the branchiostegal rays on the ceratohyal and epihyal, details of the branchial skeleton, details of the neurocranium, and number and articularion of epipleurals.

Oligoserranoides budensis shares with the Lutjanidae the number of dorsal and anal fin spines and soft rays, moderately protrusible premaxillaries, an ascending process not a separate ossification, a broadbased and not fingerlike postmaxillary process, and the presence of canines in the upper jaw.

Oligoserranoides budensis differs from the subfamily Etelinae (family Lutjanidae), which include *Aphareus*, in the predorsal formula.

Oligoserranoides budensis differs from the Apsilinae in the number of dorsal fin spines and soft rays and the number of anal fin soft rays.

Oligoserranoides budensis differs from the subfamily Lutjaninae (family Lutjanidae) which include *Pinjalo*, the subfamily Paradichthyinae (family Lutjandae) and the family Caesionidae in the absence of a posterior projection on the ectopterygoid.

Oligoserranoides budensis resembles *Lutjanus bengalensis* (Bloch, 1790), *L. boutton* (Lacepède, 1802), *L. carponotatus* (Richardson, 1842), *L. lutjanus* Bloch, 1790 and *L. madras* (Valenciennes, 1831) in a similar number of dorsal fin spines and soft rays, number of anal fin soft rays and body depth in SL (see Allen, 1985). The difference is the forked (*vs*. emarginated) caudal fin of *Ol. budensis*. It is similar in body proportions to the juveniles of several species of the Lutjanidae, *e.g. Etelis oculatus* (Valenciennes, 1828), *L. cyanopterus* (Cuvier, 1828) and *Ocyurus chrysurus* (Bloch, 1791) (see Clarke *et al*., 1997; Fahay, 2007; Victor *et al*., 2009). *Ol. budensis* differs from the juveniles of *Oc. chrysurus* of subfamily Lutjaninae in a forked (*vs*. emarginated) caudal fin (adults of *Oc. chrysurus* do have a forked caudal fin). The difference between *Oc. chrysurus* and *Ol. budensis* is the number of soft rays in the dorsal fin (Table 3). The assumed variability of *Ol. budensis* in the number of dorsal and anal fin rays is comparable to such variability in extant species of the Lutjanidae (see Allen, 1985). The pigmentation of *Ol. budensis* resembles *L. cyanopterus* (see Clarke *et al*., 1997) of comparable size but is clearly different from *L. campechanus* (Poey, 1860), *L. griseus* (Linnaeus, 1758) and *L. synagris* (Linnaeus, 1758) (see Fahay, 2007).

Oligoserranoides budensis differs from the Sparoidea in having seven (*vs*. 6) branchiostegal rays and a different predorsal formula. *Ol. budensis* differs from the Haemuloidea by having 24 (*vs*. 26-27) vertebrae, the absence of the procurrent spur, and a different predorsal formula.

Oligoserranoides budensis resembles the extant *Symphysanodon* (family Symphysanodontidae; Prokofiev, 2009; Bannikov 2010) in body proportions, meristic characters, the presence of a single dorsal fin, ctenoidal scales (Table 3), and suspensorium anatomy. *Symphysanodon* differs in 15 caudal vertebrae, the predorsal formula and two (out of three) strongly reduced epurals (Prokofiev, 2009).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The holotype of *Ol. budensis* is from Budapest, Hungary, in the Inner Carpathians, and the species was mentioned by Weiler (1933) in the Oligocene of Hungary (a more precise age was not indicated). Specimens of *Ol. budensis* occur in the Outer Carpathians, Caucasus, and in the Upper Rhine Graben (Fig. 8).

In the Outer Carpathians of Poland *Ol. budensis* is noted frequently from the Lower Oligocene, Menilite Fm., ichthyofaunal zone IPM2, and occurs in the Upper Oligocene in the same formation in ichthyofaunal zone IPM6 (Kotlarczyk *et al*., 2006). *Serranus sp*., which probably represents *Oligoserranoides* was noted in the entire succession of the Menilite Fm. correlated with the Oligocene-Lower Miocene, in ichthyofaunal zones IPM1-7 (Kotlarczyk *et al*., 2006). The material studied herein is from ichthyofaunal zone IPM2, which is correlated with the middle Rupelian, calcareous nannoplankton Biozone NP23 (see Kotlarczyk *et al.*, 2006).

Oligoserranoides budensis is also known from the Oligocene of the Outer Carpathians from the Czech Republic (Prokofiev, 2009), Romania (Paucă, 1933; Jonet, 1958, under the name *Serranus budensis*) and from Ukraine (Prokofiev, 2009; Bannikov, 2010).

In the Upper Rhine Graben, *Ol. budensis* was described from the Lower Oligocene, from the Froidefontaine locality in France, in marls with *Meletta* (*Marnes à Mélettes*) (Pharisat, 1991), as well as from coeval deposits (*Meletta*-Schichten) of the Lower Oligocene from the Frauenweiler locality in Germany (Micklich, 1998; Pharisat and Micklich, 1998).

In the Caucasus, *Ol. budensis* is noted from the upper Lower Oligocene and lower Upper Oligocene, at the Belaya River, Morozkina Balka Horizon, and at the Gumista River (Bannikov, 2010).

Ol. comparabilis is known from the Lower Oligocene of the Pshekhian Horizon, Caucasus (Danil'chenko 1960; Bannikov 2010).

Caucasoserranoides morozkiensis was described from the upper Lower Oligocene and lower Upper Oligocene of the Morozkina Balka Horizon, Caucasus (Prokofiev, 2009).

Carpathoserranoides brnoensis and *Carpathoserranoides polonicus* were described from the Oligocene of the Outer Carpathians (Prokofiev, 2009).

Pirsagatia sytchevskayae is derived from the Upper Oligocene or the Lower Miocene of the Caucasus (Prokofiev, 2002).

Difficulties in the correlation of the Oligocene deposits from the Upper Rhine Graben, Outer and Inner Carpathians, and the Caucasus (see Popov *et al.*, 2002; Prokofiev, 2009; Bannikov, 2010) do not allow for a more precise analysis of the geographic and stratigraphic distribution of *Ol. budensis*.

PALAEOBIOGEOGRAPHY

The fossil record of *Ol. budensis* indicates its wide distribution in the Paratethys (see Fig. 9) in the Lower Oligocene and in the lower Upper Oligocene strata. In contrast, *Ol. comparabilis*, known only from the Lower Oligocene of the eastern Paratethys, seems to be the Caucasian endemic species that was not a competition of *Ol. budensis*. *Ol. comparabilis* occurs earlier than *Ol. budensis* in the Early Oligocene in the eastern Paratethys. In such case, the migration of *Ol. budensis* from the Carpathian region to the eastern Paratethys seems to be possible. *Caucasoserranoides morozkiensis* and *Pirsagatia sytchevskayae* seem to be endemic species from the eastern Paratethys, whereas *Carpathoserranoides brnoensis* and *Carpathoserranoides polonicus* were endemic from the Carpathian Region of the Paratethys. Presence of species known only locally is in concordance with limited connections of the Carpathian Region and the eastern Paratethys (Fig. 9). In contrast, the wide

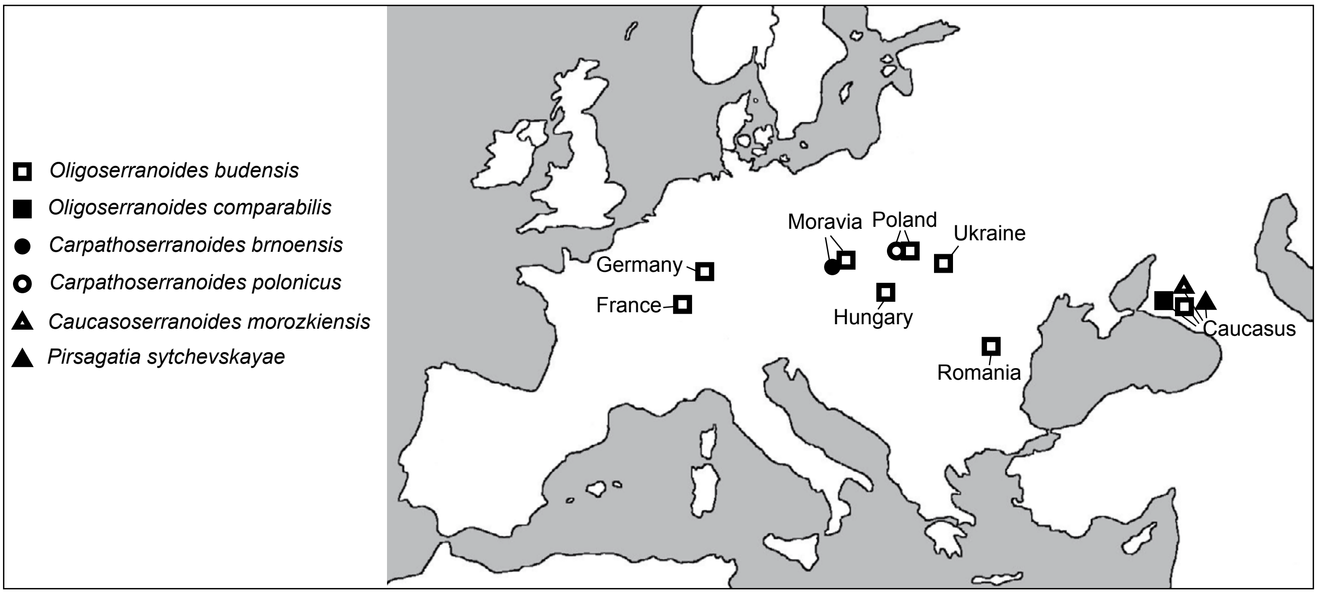

FIGURE 8. Geographic occurence of the Oligocene small percoid fishes.

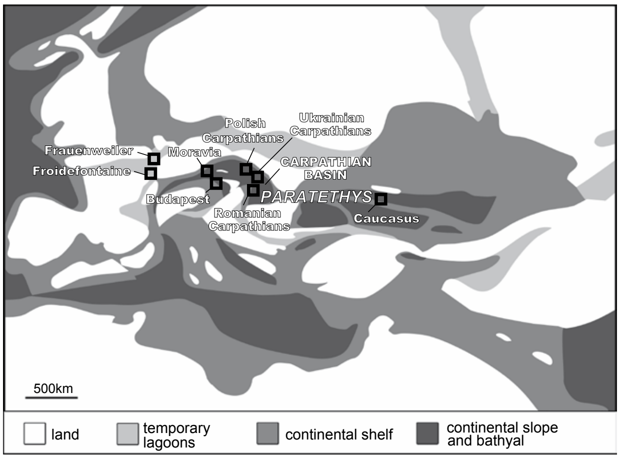

FIGURE 9. Early Oligocene (Rupelian) palaeogeography (modified from Popov *et al.*, 2002) with locations of *Oligoserranoides budensis.*

distribution of *Ol. budensis* in the Paratethys indicates the presence of connections between the Upper Rhine Graben, Carpathian Region and the eastern Paratethys in the Early Oligocene and early Late Oligocene. Future discoveries of new fossils and further studies of fishes and stratigraphy are necessary for understanding the history of these small percoid fishes.

CONCLUSIONS

We interpret the observed variability in body proportions, dentition, the predorsal formula and the number of dorsal fin spines in the studied material as variation within *Oligoserranoides budensis* (HECKEL, 1856). The species has a unique combination of features not found in any other percoid group under consideration, but it cannot be conveniently accommodated within any familial or superfamilial category. *Ol. budensis* is remarkably similar to *Lutjanus* and *Ocyurus* within the Lutjanidae.

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