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Osteological description of *Zingel balcanicus* (Teleostei: Percidae)

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Abstract: Recent field studies have shown that the survival of *Zingel balcanicus* (Karaman, 1937) was enabled in an isolated area along the Treska River. The presence of two opercular spines in *Z. balcanicus*, compared to only one in *Zingel streber*, has attracted our interest for investigating more details about osteological characters of *Z. balcanicus* in order to provide more useful anatomical data that could be of osteo-taxonomic value. A complete osteological description of *Z. balcanicus* is presented with some comparative aspects discussed. *Zingel balcanicus* shares a large number of osteological characteristics with other members of *Zingel*. However, the articular processes of the premaxillary bone, teeth in the palatine bone, opercular spination and number of precaudal centra were emphasised as stable osteo-taxonomic characters. On the other hand, the architecture of the hyomandibula, spine-like extensions of infraorbital bones, gill rakers, and independent cartilage plates and presence of "Spreitzer vertebra" were noticed as peculiar characteristics that never have been described for the genus *Zingel*.

Key words: fish; osteology; Percidae; *Zingel*

Introduction

The genus *Zingel* (Teleostei: Percidae) includes four species (*Z. asper*, *Z. zingel*, *Z. streber*, and *Z. balcanicus*) that inhabit freshwater rivers and streams. Among them, only *Z. asper* (L., 1758) has a distribution range limited to the Rhone River. *Zingel zingel* (L., 1766) and *Z. streber* (Siebold, 1963) occupy the major rivers (Danube and Dniester) in South-eastern Europe, while *Z. balcanicus*, known by common name "vretenar", is endemic to the Vardar and Treska rivers in the Republic of Macedonia (Kottelat & Freyhof 2007). The first record of *Z. balcanicus* was in the Vardar River, by Karaman (1937), and was described as a subspecies of *Aspro streber* (Siebold, 1863) — *Aspro streber balcanicus* (Karaman, 1937). The presence of *Z. balcanicus* in the Vardar River was later confirmed by Oliva (1960), as well as by Grupche & Dimovski (1973). The Treska River was also cited as one of the habitats for *Z. balcanicus* (Dimovski & Grupche 1972). Ichthyological research performed in the past 40 years in the waters of Macedonia yielded no further confirmation of the existence of *Z. balcanicus* (Kostov et al. 2010, 2011a, b; Ristovska et al. 2011).

Meanwhile, Kottelat & Freyhof (2007), based on some meristic characters (absence or low number of cheek scales and two opercular spines), gave this taxon a higher rank of distinct species — *Z. balcanicus* (Karaman, 1937). According to the IUCN Red List (IUCN 2014.1), *Z. streber* is considered "least concern" (LC) (Freyhof 2013), while the status of *Z. balcanicus* is "data deficient" (DD) (Crivelli 2006). Both species are on Anex II in the European Union Habitats Directive (92/43EEC), meaning that they are of community interest and that their conservation requires the designation of special areas of conservation.

Still, it seems impossible to assess the threat category of the species, protect its habitats, and establish conservation strategy without knowing its distribution and biology (Kottelat 1998). With the main goal of finding more data necessary to assess the threat status of *Z. balcanicus*, the Institute of Animal Science and Macedonian Fishing Federation [supported by the Global Ecology Fund (GEF)] carried out intensive field research in the rivers in the Republic of Macedonia during the period of 2012–2013. During this investigation, the presence of *Z. balcanicus* was confirmed only for the Treska River. Because of the poor data regarding its morphology, apart from several meristic data (Karaman 1937; Dimovski & Grupche 1972; Grupche & Dimovski 1973) and the doubtful taxonomic status, a reasonable number of samples were collected and used for osteological research. It already has been shown that osteological characters such as presence, number, position, and shape of certain bones of the skeleton have a taxonomic value and can be very important tools

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for exploring many areas of a taxon's biology, even for closely related species (Collette 1963; Liem 1963; Dunn 1983; Motta 1984; Wiley 1992; Bellwood 1994; Norris & Minckley 1997; Ayache & Near 2009; Bruner 2011).

Within this context, the main goal of this study was to provide a complete, detailed osteological description for *Z. balcanicus* in order to resolve its taxonomic status. The knowledge summarised from many aspects of this species' biology will underline the fundamental steps for establishing protocols for conservation and protection of its only habitat.

Material and methods

Specimens of *Z. balcanicus* were caught in the Treska River, near the vilage Belica, during September 2012 – April 2013. All specimens ($n = 22$) were caught by electro-fishing (Samus 725G) using FAME (2004) methodology and relevant standards (EN 14011-CEN, 2003). Data regarding community structure of ichthyofauna, benthic fauna, assessment of the geographical coordinates (GPS), determination of substrate type composition, temperature of the water, current, oxygen, and pH are currently being collected and will be published. The following measurements on the specimens of *Z. balcanicus* were taken during field research: total and standard length using calipers (accuracy of 0.05 mm), according to methods by Kottelat & Freyhof (2007), fin ray counts of the dorsal and anal fins, and presence/absence of the scales. Five specimens were anaesthetised using an MS 222 (3-aminobenzoic acid methanesulfonate salt, Sigma Chemical Co.) overdose; all others were released. Prior to release, scales were collected for further investigation to determine their age. These five specimens were fixed in neutral, 10% buffered formaldehyde solution and subsequently transferred to the laboratory, where, after 5 days, they were stored in 70% ethyl alcohol for further processing. Four specimens were double-stained, while one was stained only with Alizarin red S using the protocol of Hanken & Wasserzug (1981). The observations and illustrations of the skeletal structures were made using a Wild M3C microscope mounted with a camera lucida. The bone terminology largely followed that of Willey (1992), Norris (2001), and Bruner (2011). The illustrations for bones are presented with dots, while the black colour shows cartilage. All counts, observations, and drawings were made on the left body side unless stated otherwise.

Results

During the investigation period, 22 specimens with a total length (TL) ranging from 126.56–156.73 mm (mean of 141.96 ± 9.91 mm) and standard length (SL) range of 109.71–136.56 mm (mean of 123.24 ± 9.21 mm) were measured. As previously mentioned, the osteological description was based only on five specimens with a TL range of 129.97–153.62 mm (mean of 140.73 ± 10.86 mm) and SL range of 112.12–136.56 mm (mean of 122.48 ± 10.38 mm).

Neurocranium. The neurocranium of *Z. balcanicus* (Fig. 1) is composed of 11 paired (nasal, lateral ethmoid, frontal, parietal, epiotic, sphenotic, pterotic, intercalar, prootic, exoccipital, and pterosphenoid) and six unpaired bones (vomer, mesethmoid, supraoccipital, parasphenoid, and basioccipital). The paired frontals dominate, occupying the majority of the skull roof. The left and right frontals meet in the midline along most of their lengths. Each frontal bone joins the mesethmoid, nasal, and lateral ethmoid anteriorly, the supraoccipital, parietal, and pterotic posteriorly, and the seventh infraorbital, sphenotic, and pterosphenotic postero-ventrally (Fig. 1A). Laterally, the frontals carry the supraorbital sensory canal. The anterior portion of this canal continues as the nasal canal, surrounded with nasal bone. The nasal is a flatted bone, attached to the mesethmoid medially and the frontal and lateral ethmoids posteriorly. Between the left and right nasals is the mesethmoid, forming the antero-dorsal border of the neurocranium. The paired lateral ethmoids form the posterior walls of the nasal capsules. Each lateral ethmoid has two articular facets: one for articulation with the dorsal surface of the dorsal process of the first infraorbital (=lacrimal) and one for the palatine.

The dermal bones of the ventral surface of the neurocranium and ethmoid region of *Z. balcanicus* include two median bones—the vomer and parasphenoid (Figs 1B, C). The vomer broadly contacts the ethmoid cartilage on its anterior half and, posteriorly, is overlapped by the anterior end of the parasphenoid. Anteriorly, the vomer has a triangular head that bears a transverse row of very small teeth. The parasphenoid occupies much of the ventral portion of the neurocranium. It is wide and robust in its middle section between the anterior ascending processes and the more posterior prootic processes. The posterior end of the parasphenoid is forked and embraces the median anterior process of the basioccipital.

Paired parietals, pterotics, epiotics, and the median supraoccipital form much of the posterior portion of the skull roof (Fig. 1A). The parietals are relatively small, squarish elements that contact the supraoccipital medially, the frontals anteriorly, the sphenotics and pterotics laterally, and the epioccipitals posteriorly. The pterotic, occupying the postero-lateral region of the neurocranium, contacts the frontal and sphenotic anteriorly, the parietal and epioccipital medially, and the prootic and intercalar ventrally. This bone carries the pterotic canal along its dorso-lateral margin, which is connected with the extrascapular canal posteriorly and the preoperculo-mandibular canal laterally and enters in the frontal anteriorly. Ventrally, the pterotic bears the articular surface for the posterior dorsal head of the hyomandibula. The epiotic bone (=epioccipital) is located posterior to the parietal. It joins the pterotic laterally, the supraoccipital medially, and the exoccipital postero-ventrally (Figs 1A, C, Fig. 2). It provides an attachment site for the dorsal limb of the post-temporal bone on its posterior region. A second medial epioccipital process on the epiotic is present and is moderate in size. The supraoccipital is an elongate bone, and its anterior portion is partially overlapped by the posterior portion of the frontals. It makes contact with the parietal and epioccipital laterally and the exoccipital ventrally. It bears a supraoccip-

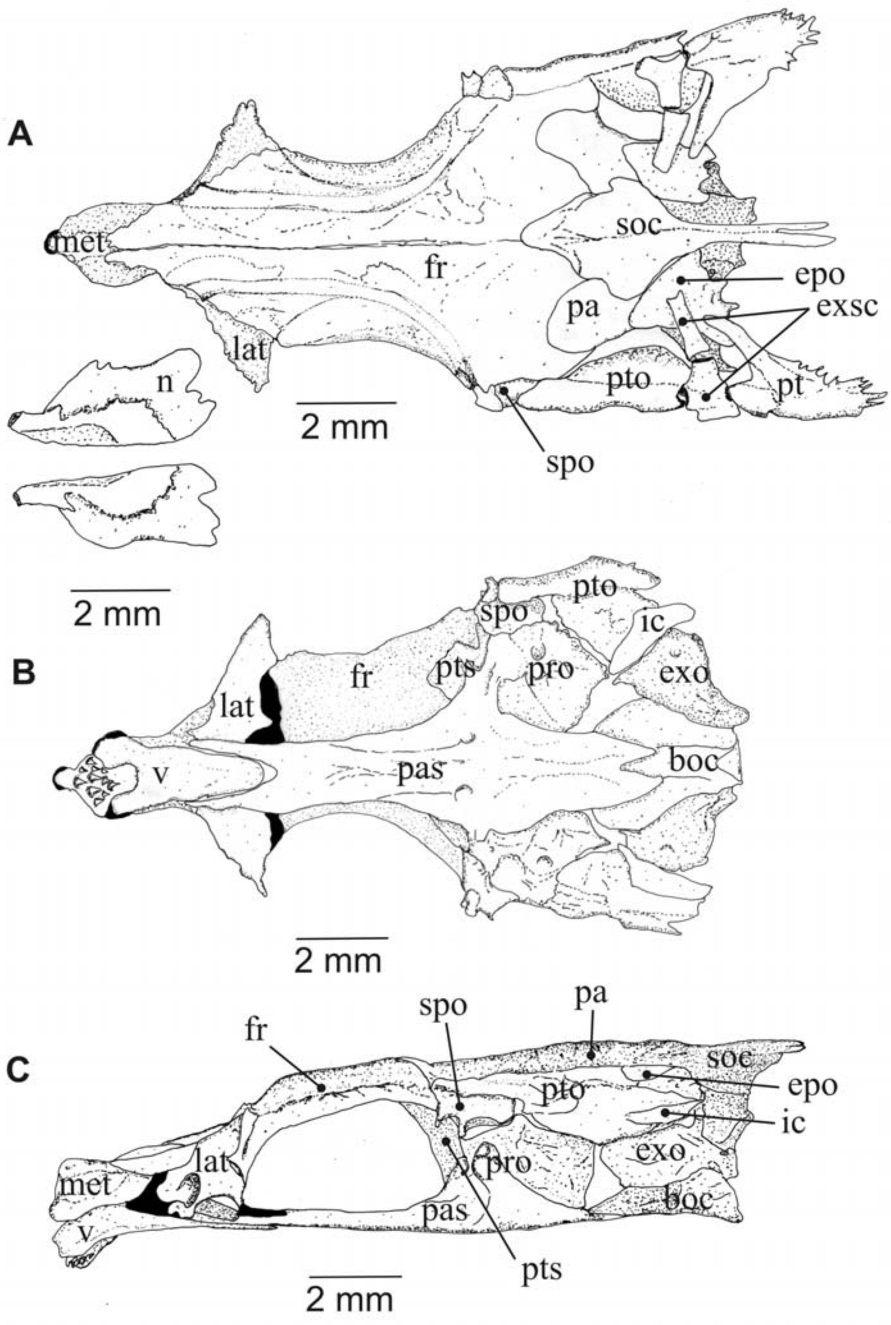

Fig. 1. Neurocranium of *Z. balcanicus*: A – Dorsal view (including the nasal, extrascapular and post-temporal bone); B – Ventral view; C – Lateral view. Abbreviations: boc – basioccipital; epo – epioccipital; exo – exoccipital; exsc – extrascapulars; fr – frontal; ic – intercalar; lat – lateral ethmoid; met – mesethmoid; n – nasal; pa – parietal; pas – parasphenoid; pro – prootic; pt – post-temporal; pto – pterotic; pts – pterosphenoid; soc – supraoccipital; spo – sphenotic; v – vomer.

ital crest that is bi-lobed on its posterior end (Fig. 1A, Fig. 2).

The exoccipital covers much of the lower posterior region of the neurocranium. It joins the supraoccipital, the epiotic, and intercalar dorsally, the prootic anteriorly, and the basioccipital ventrally. Posteriorly, they form the dorso-lateral components of the occipital condyle. Ventrally, the exoccipitals are greatly expanded and contact the basioccipital. The basioccipital occupies the postero-ventral region of the neurocranium. Anteriorly, it has a sharp median process that interdigitates with the posterior processes of the parasphenoid. It is also bordered by prootic and exoccipital bones and has a condyle for articulation with the first vertebra.

The intercalar is a small, flat bone that lies on the postero-lateral region of neurocranium. It makes contact with the exoccipital postero-medially, pterotic dorsally, and prootic anteriorly, and it receives the ventral arms of the post-temporal. The sphenotic is located on the postero-dorsal corner of the orbit. It makes contact with the frontal and pterotic dorsally, the prootic ventrally, and the pterosphenoid antero-medially. The articular surface of the anterior dorsal

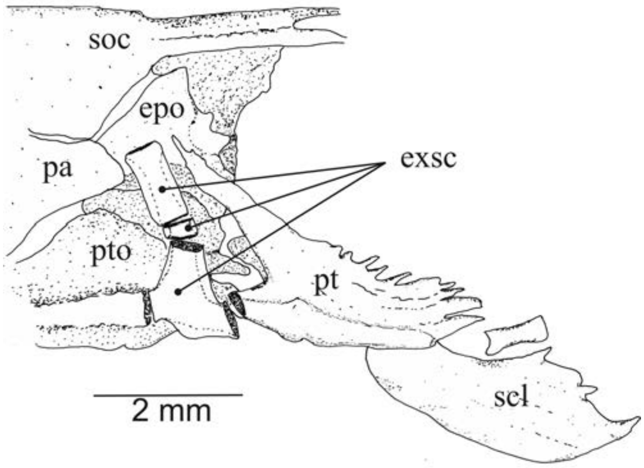

Fig. 2. Posterior region of skull in *Z. balcanicus* in lateral view. Abbreviations: cfs – canal of the first lateral line scale; epo – epioccipital; exsc – extrascapular; pa – parietal; pt – post-temporal; pto – pterotic; scl – supracleithrum; soc – supraoccipital.

head of the hyomandibula is entirely within the sphenotic. The prootics are the largest bones on the ventral surface of the braincase (Fig. 1B). It joins the sphenotic, pterotic, and intercalar dorsally, the exoccipital and basioccipital posteriorly, the parasphenoid ventrally, and the pterosphenoid and basisphenoid anteromedially. The pterosphenoid forms the postero-dorsal wall of the orbit and joins the frontal dorsally, the sphenotic laterally, and the prootic ventrally. At the skull of *Z. balcanicus*, the basisphenoid and orbitosphenoid are absent.

Two extrascapular bones carry the sensory canal; the ventral is an inverted "Y" shape, while the dorsal is tube-like (Fig. 1A). In one of the examined specimens, three extrascapulars were registered (Fig. 2).

Infraorbital bones and sclerotic ring. The infraorbital series are composed of one lacrimal and six infraorbital bones and form a serial, tubular structure for the infraorbital sensory canal (Fig. 3). The lacrimal (infraorbital 1) is large, long, and significantly deep in its anterior part and has a clear dorsal process for articulation with the lateral ethmoid. It joins the second infraorbital posteriorly. Compared to the first infraorbital, infraorbitals 2 and 3 are small, short, and quadrate. Their depth equals the depth of the posterior end of lacrimal. Infraorbital 2 is widely overlapped by the lacrimal. Both bones bring a short spine on their ventral side orientated ventrally. The remaining infraorbitals are in the vertical position. In four of the examined specimens, infraorbital 7 was the smallest with a tubular shape (Fig. 3B). In only one of the samples,

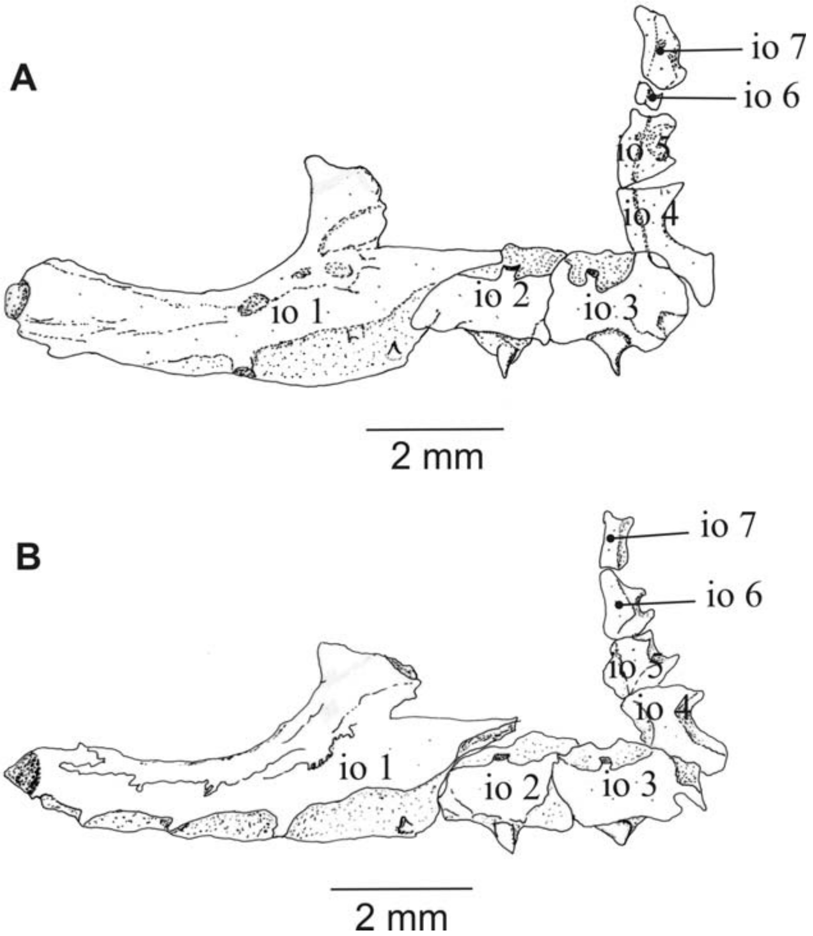

Fig. 3. Variation (A; B) in infraorbital bones of *Z. balcanicus* in lateral view. Abbreviations: io – infraorbital.

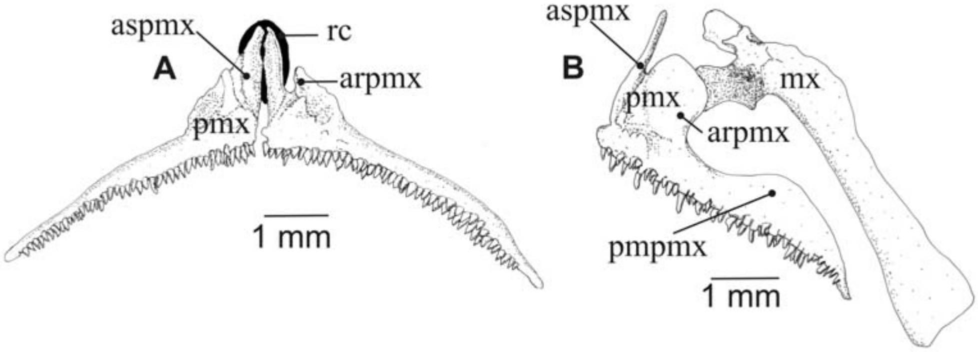

Fig. 4. Upper jaw in *Z. balcanicus*: A – Anterior view; B – Lateral view. Abbreviations: arpmx –articular process of premaxilla; aspmx – ascending process of premaxilla; mx – maxilla; pmpmx –postmaxillary processes of premaxilla; pmx – premaxilla; rc – rostral cartilage.

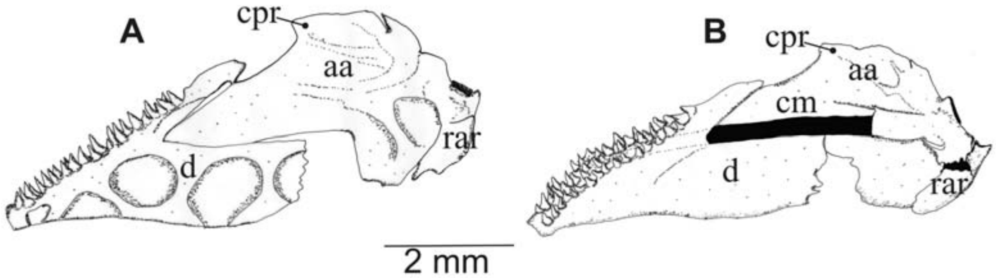

Fig. 5. Lower jaw in *Z. balcanicus*: A – Lateral view; B – Medial view. Abbreviations: aa – angulo-articular; cm – coronomeckelian cartilage; cpr – coronoid process; d – dentary; rar – retroarticular.

infraorbital 6 had smaller dimensions than infraorbital 7 (Fig. 3A). The infraorbital 7 (=dermosphenotic) is loosely connected to the frontal and passes over the sphenotic; its canal is connected to the latero-sensory canal of the frontal. The sclerotic cartilage supports two ossifications, positioned anteriorly and posteriorly in the orbit.

Jaws, suspensorium, and opercular bones. The *upper jaw* consists of paired maxillae and premaxillae. They exhibit the generalised percoid type. The premaxilla, which is relatively short, has a prominent ascending process that articulates with the rostral cartilage, an articular process, and a developed postmaxillary process (Fig. 4). The articular process is almost square-shaped, with height almost equal to width. On the ventral border of the premaxillary, 3–4 rows of conical teeth are present, which almost reach the end of the bone. The maxilla is composed of a head, which bears the premaxillary condyle ventro-medially. It articulates with the articular process of the premaxilla and cranial condyle dorsally and articulates with the antero-lateral face of the rostral region of the neurocranium.

The *lower jaw* contains dentary, angulo-articular, and retroarticular bones (Fig. 5). The dentary is a V-shaped bone with two rami. The dorsal one bears conical teeth in 2–3 rows that stop before the posterior end. The ventral ramus supports the anterior portion of the mandibular sensory canal opened with five enlarged sensory foramina (Fig. 5A). The slot between these two rami is occupied by the angulo-articular bone. The posterior portion of the lower jaw is composed of the angulo-articular and the retroarticular (Fig. 6). The angular portion of this bone supports the posterior portion of the mandibular sensory canal and possesses the coronoid process on its dorsal part, while the articular portion forms the facet for articulation with the quadrate. It also joins the retroarticular postero-ventrally. The coronoid process does not meet the dorsal ramus of the dentary bone. The retroarticular is small, closely adherent to the ventro-caudal edge of articular bone. The coronomeckelian bone is absent.

The *suspensorium* is composed of the palatine, entopterygoid, ectopterygoid, metapterygoid, quadrate, symplectic, hyomandibula, and preopercle. The palatine is the most anterior bone of the suspensorium and bears an anterior cartilaginous cap. The anterior portion of the palatine expands and articulates with the head region of the maxilla antero-ventrally. There are few conical small teeth (12–18) located only on the most antero-ventral portion of the palatine. There is a slight curve to the antero-dorsal part of the palatine, at the level of the lateral ethmoid, where they articulate. Posteriorly, the palatine joins the entopterygoid and ectopterygoid. The entopterygoid is a large, thin bone. Its ventral part follows the cartilage of the palatoquadrate; medially, it becomes thin and supports the orbit, whereas, posteriorly, it meets the metapterygoid bone. The dermal ectopterygoid contacts the antero-dorsal part of the quadrate and lies lateral to the cartilaginous bridge, between the quadrate and palatine. The metapterygoid is a roughly rectangular bone. It lies antero-dorsal to the hyomandibula and postero-ventral

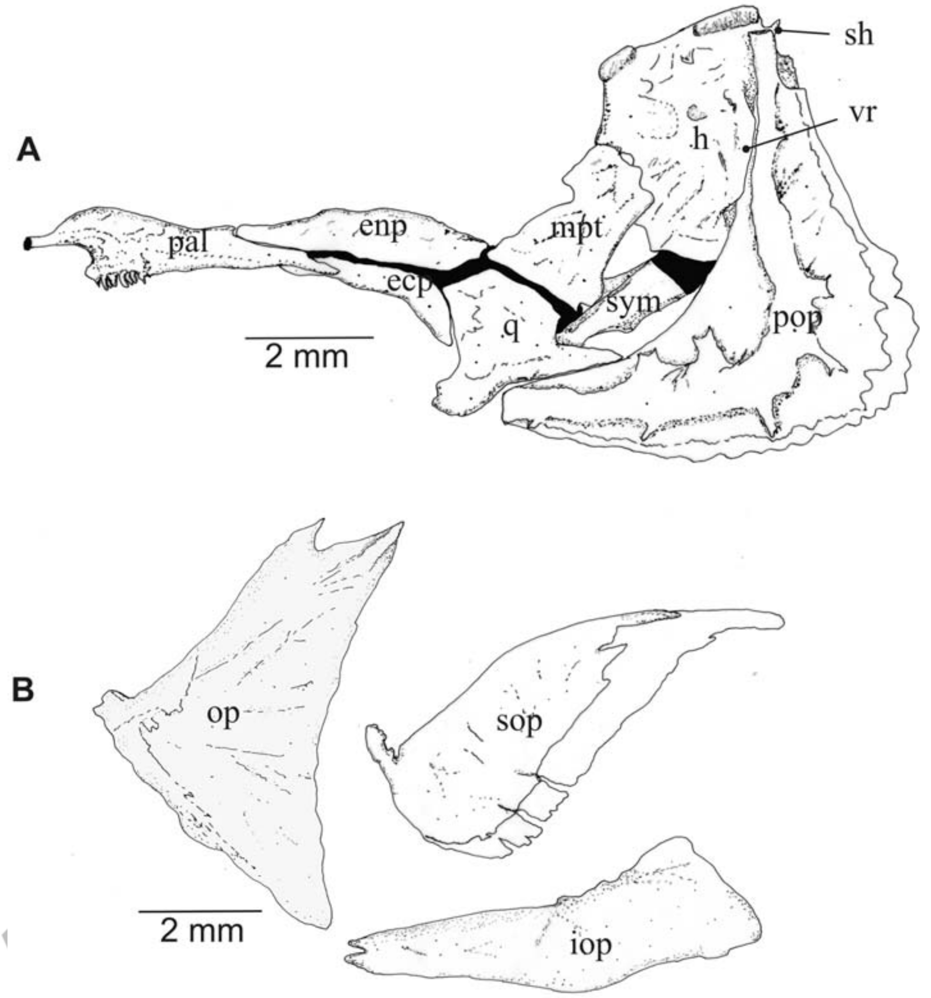

Fig. 6. Structure of viscerocranium in *Z. balcanicus*: A – Suspenzorium; B – Opercular bones. Abbreviations: ecp – ectopterygoid; enp – entopterygoid; h – hyomandibula; iop – interopercle; mpt – metapterygoid; op – opercle; pal – palatine; pop – preopercle; q – quadrate; sh – spur; sop – subopercle; sym – symplectic; vr – vertical ridge.

to symplectic bone. The quadrate is approximately triangular in shape, having a large condyle for articulation with the angulo-articular antero-ventrally. Its posterior process is sharp, long, straight, and directed posteriorly. This part of the quadrate forms the concavity that articulates with the symplectic and lies dorsally to the anterior arm of the preopercular bone.

The symplectic has a cartilaginous cap on its ventral tip and a cartilaginous socket for articulation with the interhyal dorsally. The anterior half of this bone rests in a deep concavity on the medial surface of the quadrate; it is interdigitate with the metapterygoid antero-dorsally. The hyomandibula is a large bone with a broad dorsal articulatory head where it meets the neurocranium. At this junction, the hyomandibula articulates with the sphenotic and pterotic. The opercular condyle is pronounced but almost completely hidden in lateral view by the opercle and preopercle. Between this condyle and the postero-dorsal corner of the hyomandibula, there is a prominent membranous posterior extension (=spur) (Fig. 6A). In all examined specimens, a sharp vertical ridge passes down the posterior border of the hyomandibula, covering the anterior portion of the preopercle. The hyomandibula contacts the metapterygoid antero-ventrally, while with its ventral portion is in contact with the symplectic and interhyal bones via cartilage. The main axis of the hyomandibula is oriented vertically.

Opercular bones include the preopercle, opercle, subopercle, and interopercle. The preopercle (also as part of the suspensorium) surrounds the preopercular sensory canal (Fig. 6A). The canal is continuous with that of the angulo-articular antero-ventrally and that of the pterotic bone dorsally. Anteriorly, it is attached to the hyomandibula and quadrate and, posteriorly, with the opercle, subopercle, and interopercle. The posterior margin of the bone is membranous and serrated on its horizontal and vertical shafts (Fig. 6B). The operculum is a large triangular bone, joining the hyomandibula and preopercle anteriorly and the subopercle ventrally. There are two distinct spines on the dorso-posterior margin. The subopercle is roughly V-shaped, positioned medial to both the opercle and the interopercle. The postero-dorsal margin of the subopercle bears a distinct dorsal extension. The posterior margin of the bone is membranous. The thin, flat, triangu-

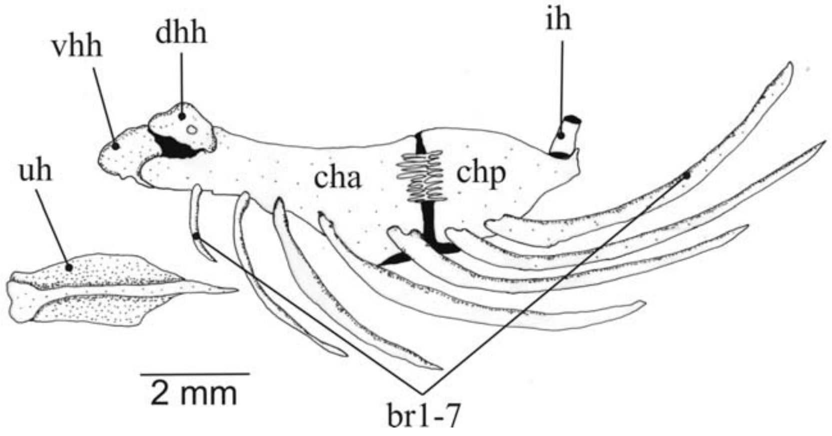

Fig. 7. Ventral hyoid arch with branchiostegals in lateral view and urohyal in dorsal view of *Z. balcanicus*. Abbreviations: br – branchiostegal; cha – anterior ceratohyal; chp – posterior ceratohyal; dhh – dorsal hypohyal; ih – interhyal; uh – urohyal; vhh – ventral hypohyal.

lar interopercle bears a well-developed articular socket that is connected with the retroarticular. The ventral portion of the bone has smooth margins.

Ventral portion of the hyoid arch. The ventral portion of the hyoid arch is composed of the basihyal, dorsal, and ventral hypohyals, the anterior and posterior ceratohyals, the interhyal, and the urohyal (Fig. 7). The basihyal is a simple rod-like bone with anterior and posterior cartilaginous tips associated with the dorsal surface of the first basibranchial. The hypohyal, occupying the anterior portion of the hyoid arch, is composed of two elements: dorsal and ventral hypohyals. The hypohyals contact one another medially and form a blunt anterior margin of the hyoid arch. The dorsal hypohyal contacts the anterior ceratohyal through a cartilage-filled suture. The anterior ceratohyal is the largest element of the ventral hyoid arch and is hatchet-shaped in lateral view, with a deep posterior portion and narrow anterior portion. The posterior ceratohyal is roughly triangular in shape. Its posterior portion bears a small dorsally directed process that articulates with the interhyal. Both the anterior and posterior ceratohyals support the seven branchiostegals. The anterior supports five, while the posterior supports two branchiostegal rays. The proximal ends of the branchiostegal rays are extended and spatulated. The interhyal is a short, rod-like bone with cartilage at both its proximal and distal tips. It articulates with the more dorsal portion of the hyoid arch, at the remnant of the hyosymplectic cartilage, posterior to the dorsal end of the symplectic and ventral to the hyomandibular. The urohyal is a roughly triangular element, shaped like an inverted "T" in cross-section, lying on the midline below the basibranchials. It has a robust anterior head that contacts the anterior ends of the left and right anterior ceratohyals and is attached to the hypohyals.

Gill arches. The branchial arches are composed of the basibranchials, hypobranchials, ceratobranchials, epibranchials, and infrapharyngobranchials (Fig. 8). The basibranchial skeleton of the gill arches consists of two copulae. The anterior basibranchial copula supports three distinct basibranchial ossifications (bb 1–3). The posterior basibranchial copula is not ossified. The first basibranchial is a pointed, rod-like bone that is inserted into the lower portion between both dorsal hypohyals. Anteriorly, the second basibranchial articulates with the first basibranchial as well as with the first hypobranchial; it articulates caudally with the third basibranchial and the second hypobranchial. The third basibranchial is sandwiched laterally by the third hypobranchial, anteriorly by the second basibranchial and second hypobranchials, and caudally by the posterior basibranchial copula. The hypobranchials are situated between the basibranchials and the ceratobranchials. Of them, hypobranchials 1 and 2 are more or less rectangular. Hypobranchial 3 has a tapered anterior extension that runs latero-ventrally to bb 3, while, posteriorly, it is broad and round. The anterior four ceratobranchials (cb 1–4) are highly elongated bars that support the gill rakers. Ceratobranchial 5 is widest anteriorly and supports well-developed conical teeth on its midsection, arranged into more or less regular rows. Ceratobranchials 1–3 articulate with their corresponding hypobranchial facets anteriorly and epibranchial facets posteriorly. Anteriorly, the fourth ceratobranchial is attached to the posterior basibranchial copula and, posteriorly, to the fourth epibranchial. All gill rakers of *Z. balcanicus* are equal in size, lying on the latero-ventral portion of ceratobranchials 1–4. They are shaped like hemispheres that bear small denticles.

The epibranchials are situated between the infrapharyngobranchials and the ceratobranchials (Figs 8A, B). Epibranchial 4 is the shortest, while epibranchial 1 the longest. Epibranchial 1 bears a well-developed uncinate process that articulates with infrapharyngobranchial 2. The anterior end of epibranchial 2 is broad, with its cartilage tip contacting cartilaginous prominences of both infrapharyngobranchials 2 and 3. The third epibranchial bears a tooth plate on the ventral surface. Only in two of the examined specimens there was a presence of the independent (accessory) cartilage between the uncinate process of epibranchial 1 and infrapharyngobranchial 2 (Fig. 8B). The infrapharyngobranchials are composed of one car-

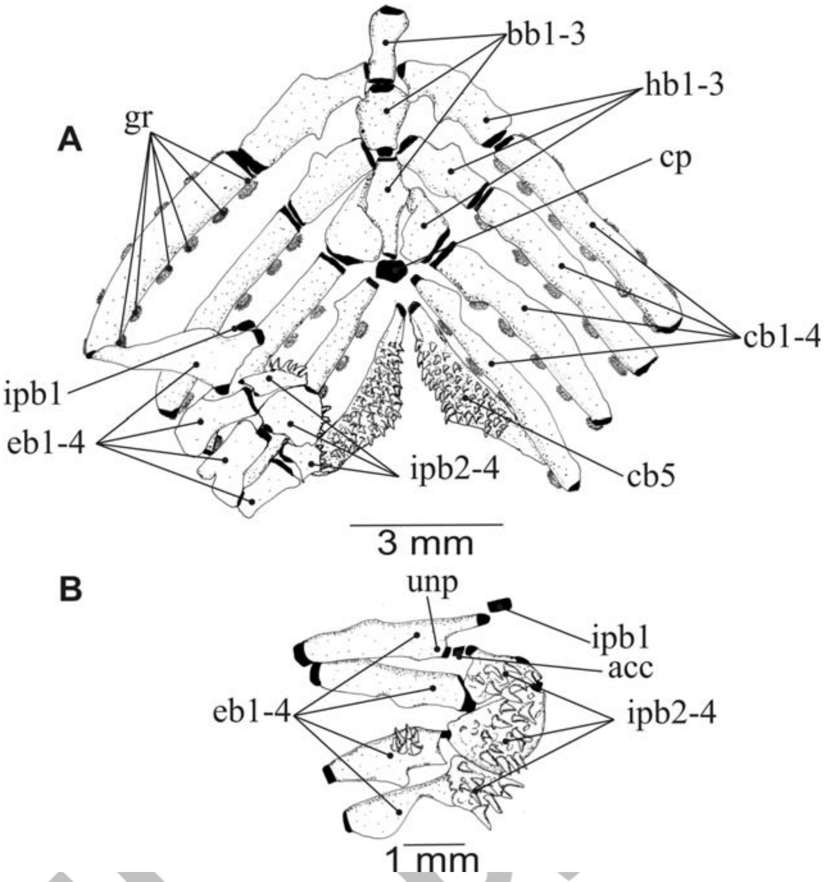

Fig. 8. Gill arch elements of *Z. balcanicus*: A – Dorsal view; B – Ventral view. Abbreviations: acc – accessory cartilage; bb – basibranchial; cb – ceratobranchial; cp – copula posterior; eb – epibranchial; gr – gill rakers; hb – hypobranchial; ipb – infrapharyngobranchial; unp – uncinate process of eb1.

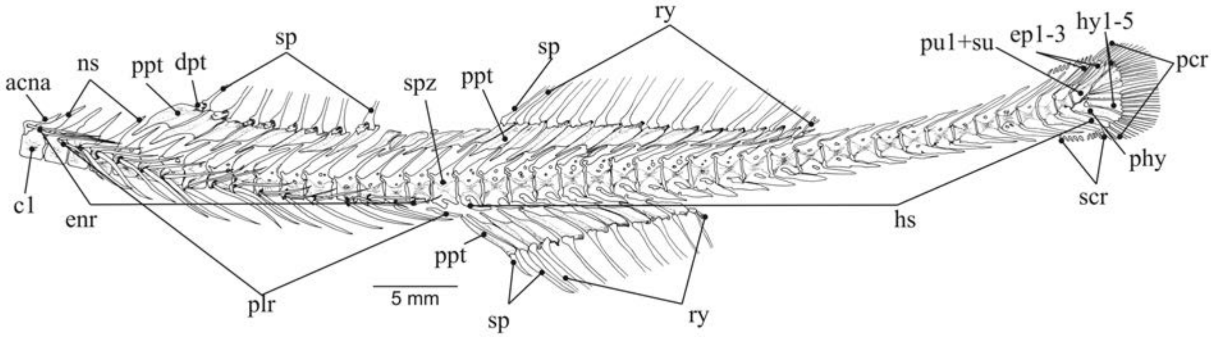

Fig. 9. Postcranial skeleton of *Z. balcanicus.* Abbreviations: acna – accesory neural arch; c –centrum; dpt – distal pterygiophore; enr – epineural ribs; ep – epural; hs – hemal spine; hy – hypural; ns – neural spine; pcr – principal rays; phy – parhypural; plr – pleural ribs; ppt – proximal pterygiophore; pu – preural centrum; ry – rays; scr – procurrent rays; sp – spine; spz – Spreitzer vertebrae; su – stegural.

tilage piece and three toothed bones. The first infrapharyngobranchial, which is vertically oriented cartilage, makes contact with the parasphenoid anteriorly and with the first epibranchial posteriorly. The second is connected to the first epibranchial anteriorly, the second epibranchial laterally, and the third infrapharyngobranchial posteriorly. The largest (third) infrapharyngobranchial articulates with epibranchials 2–3 laterally and with infrapharyngobranchial 4 posteriorly.

Vertebral column. The total number of vertebrae ranged from 44–45, including the centrum of the accessory neural arch in two of the examined specimens (Fig. 9). This centrum is smaller than the other centra, and the neural arch above it is autogenous. The vertebrae are composed of 18–20 precaudal (=abdominal) and 24–25 caudal elements.

The neural arches bear short anterior and posterior zygapophyses, which articulate with those of adjacent vertebrae. In the specimens where the accessory neural arches are without their own centrum, they attach to the body of the first centrum (Fig. 9). The neural spines in all centra (including the accessory neural arch) are

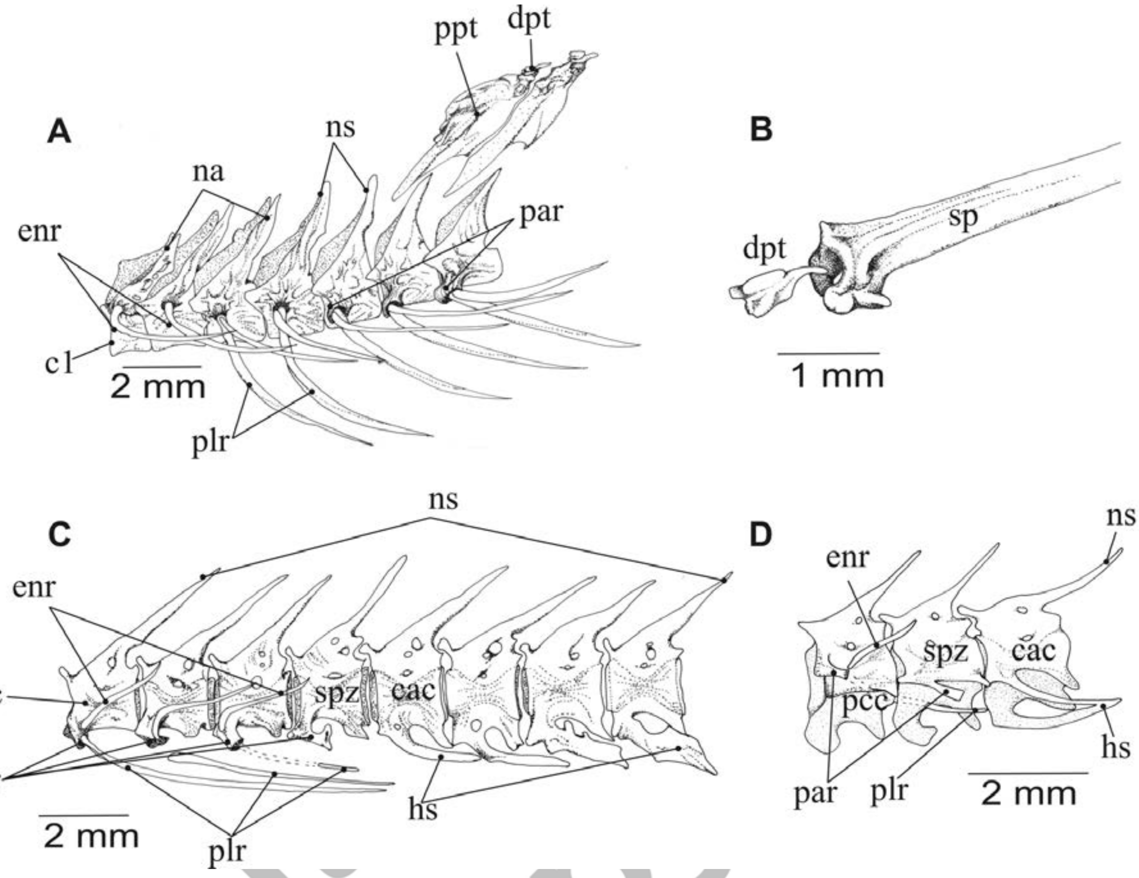

Fig. 10. Structure of vertebral column and associated elements in *Z. balcanicus*: A – First precaudal centra; B – Articulation of spine with distal pterygiophore in first dorsal fin; C – Last precaudal and first caudal centra; D – Spreitzer vertebrae in ventro-lateral view. Abbreviations: c – centrum; cac – caudal centrum; dpt – distal pterygiophore; enr – epineural ribs; hs – hemal spine; na – neural arch; ns – neural spine; par – parapophysis; pcc – precaudal centrum; plr – pleural ribs; ppt – proximal pterygiophore; sp – spine; spz –"Spreitzer" vertebrae.

well developed except for those on the final two caudal centra. Only in two of the examined samples the neural arches of the first three centra did not form neural spines. The neural spines in the anterior part of the column are elongate and nearly vertical, while they are inclined and shorter in the caudal region. There is 1–2 foramina on each side of an individual vertebra at the base of the neural spines.

The first 1–2 vertebral bodies are without pleural ribs. They possess only epineural ribs that lie on the antero-lateral surface of the centrum, connected to the bases of the neural arches. The accessory neural arch also possesses epineural ribs connected to their base. All ribs are elongated, gently curved elements attached to the posterior face of the parapophysis, ventrally of the epineurals. Parapophyses become longer and more pronounced posteriorly along the vertebral column beginning at the third vertebra; caudally, they smoothly turn into the series of hemal arches and spines. Only in one of the examined specimens the pleural ribs begin from the second centrum (Fig. 9). At the first few abdominal centra (c3–c6), parapophyses extend dorso-laterally from the anterior portion of the centrum. From centrum 7, until the end of the last precaudal centra, the parapophyses are orientated ventro-laterally. The final two ribs are short, stick-like bones (Fig. 10C). In two of the examined specimens, the last abdominal centra possess elongated parapophyses without pleural and epineural ribs [="Spreitzer vertebrae", according Bruner (2004, 2011)] (Figs 10C, D). Starting from the first precaudal centra and proceeding further caudally, the hemal spines are more posteriorly inclined, thus forming a protective, posterior wall for the abdominal cavity. In some centra, on the base of hemal arches, there exist one or two foramina (Fig. 9).

Dorsal and anal fins. In *Z. balcanicus*, there are two dorsal fins composed of pterygiophores, spines, and branched fin rays (Fig. 9). The *first dorsal fin* is constructed from eight proximal and distal pterygiophores bearing eight spines. In three of the examined samples, the first proximal pterygiophore is inserted between the fourth and fifth neural spines, while in the others they are inserted between the fifth and sixth neural spines (Fig. 10A). All proximal pterygiophores have equal sizes. The distal radials of the first dorsal fin are posteriorly pointed to insert into the foramen of subsequent dorsal spines (Fig. 10B). The *second dorsal fin* bears only one spine followed by 14–15 branched dorsal fin rays connected to the proximal pterygiophores via small distal pterygiophores. The final two are split up to their dorsal parts and lie on the same, the smallest pterygiophore (=stay). Between the two sets of dorsal

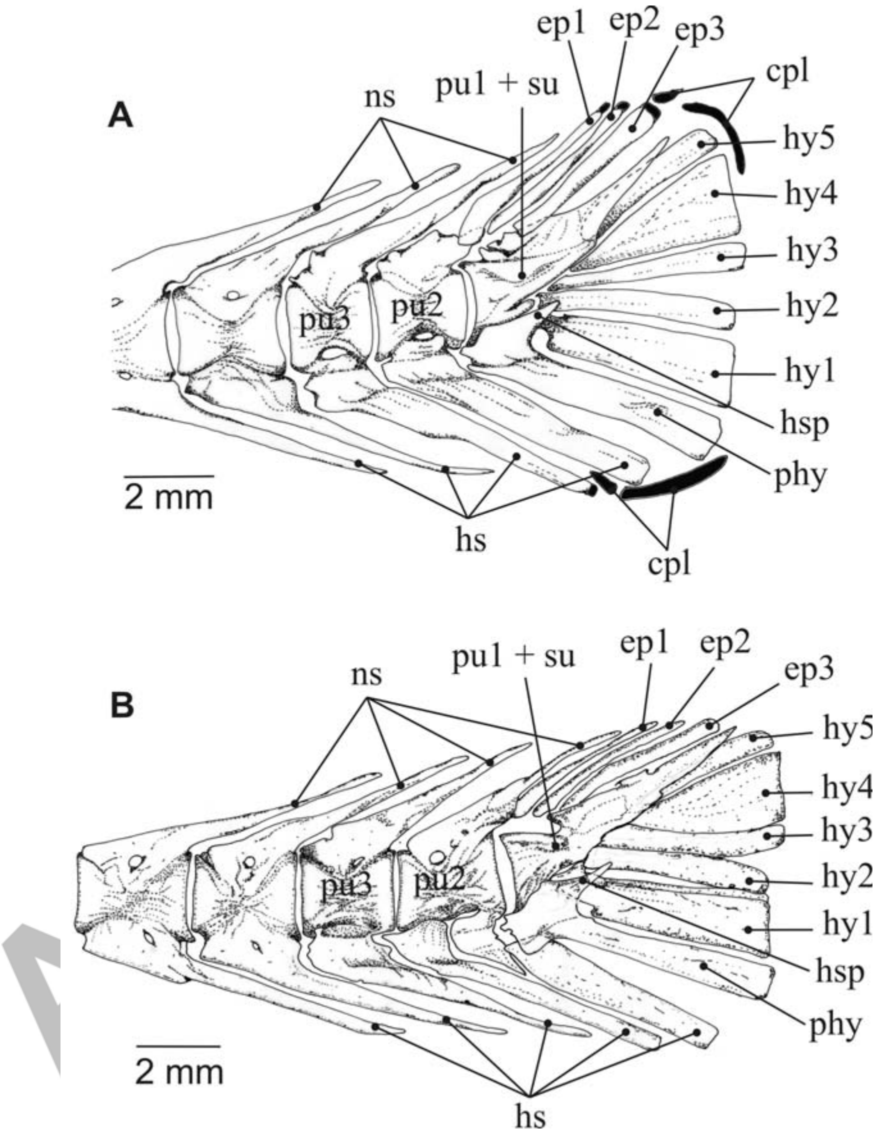

Fig. 11. Variation in the caudal fin skeleton in *Z. balcanicus*: A – Double-stained specimens; B – Specimen stained with Alizarin red S. Abbreviations: cpl – cartilage plate; ep – epural; hs – hemal spine; hsp – parhypurapophysis; hy – hypural; ns – neural spine; phy – parhypural; pu – preural centrum; su – stegoural.

fin proximal pterygiophores is a set of 4–5 free pterygiophores. The dorsal pterygiophore formulae (Fig. 9 and Fig. 10B) is ////1/1/-; /////1/1/- or /////1/1/-; /////1/1/- ("/" represents the neural spine of the precaudal centrum, and "1" means that the next neural spine has a proximal pterygiophore with an attached spine inserted after it).

The *anal fin* consists of two spines and 9–10 branched fin rays, articulating with 10–11 proximal pterygiophores via small distal pterygiophores. The first spine is half of the length of the second spine. Each spine lies on its own proximal pterygiophore. The first anal proximal pterygiophore is inserted into the front of the first haemal spine (c18–c19 centra). The size of the pterygiophores, as in the case of the second dorsal fin, is reduced from the anterior to caudal direction. However, the first anal proximal pterygiophore is about the same length as the second one but is relatively thin. On the last, smallest pterygiophore – stay, two branched rays are articulated.

Caudal skeleton. In the caudal skeleton, there are five autogenous hypuralia, a parhypural with a long and thin parhypurapophysis, and a stegural fused with the preural centrum 1, preural centrum 2, and three epiurals (Fig. 11). The caudal fin itself is composed of 41–42 fin rays, of which 22 are branched (principal rays) (Fig. 9). Dorsally, the caudal fin rays are supported by the neural spines of preurals 3 and 4, the epiurals, the posterior portion of the preural 1+stegural complex, and the posterior hypurals (hy3–5). The ventral caudal fin rays are supported by the parhypural, hypurals (1–2), and the haemal spine of preurals 2–4.

Hypurals 1 and 4 are wide, while the others are narrow. All are located on the postero-ventral margin of the preural 1+stegural complex. There are three epiurals, lying above the preural 1+stegural complex. All of them possess distal cartilaginous edges. There is individual variation regarding presence of the autogenous neural and haemal spines in the preural centrum 2. In most cases, the preural centrum 2 possess only neural

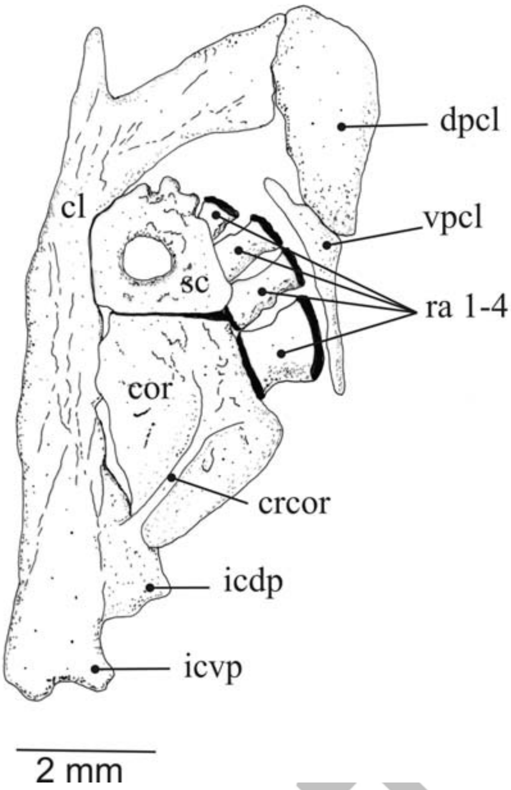

Fig. 12. Pectoral girdle of *Z. balcanicus* in medial view. Abbreviations: cl – cleithrum; cor – coracoid; crcor – crest of coracoids; dpcl – dorsal postcleithrum; icdp – dorsal process on posterior margin of internal lateral crest of cleithral shaft; icvp – ventral process on internal lateral crest of cleithral shaft; ra – pectoral radials; sc – scapula; vpcl – ventral postcleithrum.

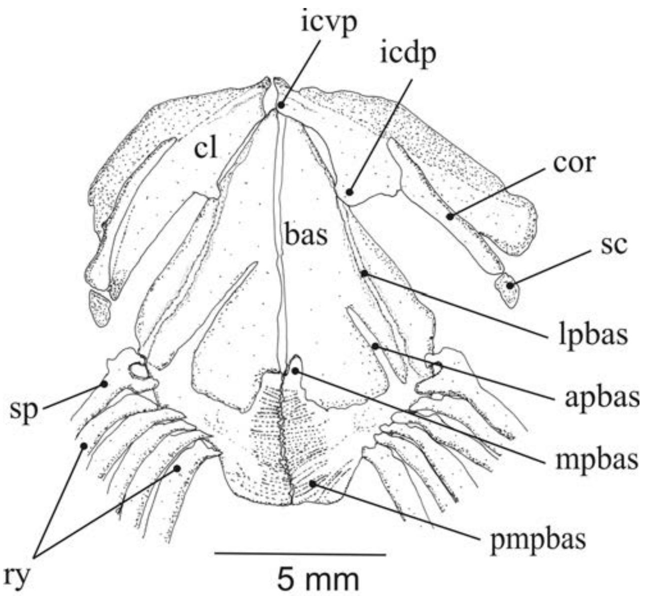

Fig. 13. Pelvic and pectoral girdle of *Z. balcanicus* in ventral view. Abbreviations: apbas – anterior process of basipterygium; bas – basiptergyium; cl – cleithrum; cor – coracoid; icdp – dorsal process on posterior margin of internal lateral crest of cleithral shaft; icvp – ventral process on internal lateral crest of cleithral shaft; labas – lateral process of basipterygium; mpbas, medial processus of basipterygium; pmpbas – processus medialis posterioris of basiptergium; ry – rays; sc – scapula; sp – spine.

arches without a neural spine and haemal arches with a haemal spine (Fig. 11A). In one of the specimens, there are two haemal spines; the first one is associated with pu2, while the second is autogenous (Fig. 11B). This preural centrum 2 bears one neural spine associated with this centrum. There are usually a few cartilage plates lying postero-dorsally to the epiurals and final hypurals as well as ventro-caudally to the last haemal spine and parhypural.

Pectoral girdle and fin. The pectoral fin is composed of one spine and 14–15 branched rays, all associated with the radial elements, decreasing in size antero-dorsally to postero-ventrally. The chondral components of the pectoral girdle include the scapula, the coracoid, and four radials, while the dermal ones consist of the cleithrum, supracleithrum, two postcleithra, and the post-temporal (Fig. 12).

The scapula is a small, somewhat square bone that entirely encloses the scapular foramen. It is overlapped by the cleithrum anteriorly and is synchondrally joined to the coracoid ventrally. The postero-dorsal corner of the bone bears a "saddle-shaped" condyle that articulates with the pectoral spine. The coracoid is an elongated element that tapers to an anterior point. With its long process (crest), it articulates with the inner side of the ventral branch of the cleithrum, slightly behind its anterior end. There are four ossified pectoral radials. The most dorsal radial is the shortest, and the fourth is the longest. In lateral view, the centre of the fourth radial element is more than twice the height of the centre of the third radial element. Two radials articulate with the scapula, one to the junction of the scapula and coracoid, and one to the coracoid.

The cleithrum, a long, gently curved element, makes contact with the supracleithrum and dorsal postcleithra dorsally, the coracoid and the scapula posteriorly, and the basipterygia ventrally. The antero-ventral portion bears two processes: ventral and dorsal. The ventral one (named as a ventral process of the internal lateral crest of the cleithral shaft) meets the same one from the opposite sides, in the ventral midline of the body, and lies ventrally to the anterior portion of basipterygial bone. The dorsal process (named as a dorsal process of the internal lateral crest of the cleithral shaft) articulates with the lateral face of the basipterygia. There are two postcleithra: a dorsal, leaf-like one and a ventral, rib-like-shaped one. The posterior edge of dorsal postcleithrum is smooth. The supracleithrum is a leaf-like bone attached to the post-temporal dorsally and the cleithrum ventrally (Fig. 12). The postero-dorsal margin of the supracleithrum is serrated. There is no tube for a lateral line on it. Each post-temporal bears a prominent dorsal limb that articulates with the epiotic (Fig. 12). The ventral limb of the post-temporal articulates with the intercalar. Compared to the dorsal limb, it is shorter and grades into the main body of the post-temporal. The lateral-line canal on the post-temporal is directly connected to the first lateral-line scale. The post-temporal is serrated on the postero-ventral border.

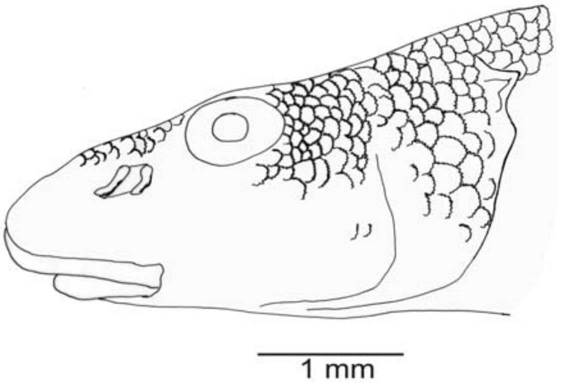

Fig. 14. Scales on the head of *Z. balcanicus* in lateral view.

Pelvic girdle and fin. The pelvic bones are elongate and triangular-shaped. They are approximated by their ventro-medial ridges and united by their inner margins at the base of each basipterygial plate (Fig. 13). The lateral process, almost as long the lateral ridge, is present on the ventral surface of the basipterygium. In each pelvic plate, the anterior process, in ventral view, is nearly half the length of the lateral process. The processus medialis, posterior of each plate, is parallel and has rounded posterior margins. Both right and left medial processes in ventral view are parallel. The base of the basipterygium on its ventral surface is an articulation place for the pelvic fin. There is one sharp hard spine and five branched rays in every pelvic fin.

Squamation. The entire body is covered with scales except on the following places: surface of the occipital bone; region between the pectoral fins; cheeks [few scales were detected along the posterior lower edge of orbit but not under the central and anterior parts of the eye (Fig. 14)]; and midline belly (excluding 2–3 rows of scales in front of the urogenital papilla). The lateral line canal is covered with 73–84 + 3–6 scales (mean 79+5). Scales above (5–7, mean 6) and below (12–15, mean 13.5) the lateral line were also counted. All specimens showed the same pattern of pigmentation presented by five regular dark, transverse bands, not including the dark spot on the head.

Discussion

Fin ray counts, especially the dorsal ones, are characters of great taxonomic value within the genus *Zingel* but only for separating *Z. zingel* from the other three members. Namely, a number of 12–15 spines in the first dorsal fin is diagnostic for *Z. zingel*, whereas a 7–10 is typical for *Z. asper*, *Z. balcanicus*, and *Z. streber* (Kottelat & Freyhof 2007). The observation of the data considering ray counts in *Z. balcanicus* and *Z. streber* indicates great variation, not only for the dorsal fins but for the anal fins, as well (Table 1). Because of these variations, ray counts cannot lead to stable taxonomic distinction between these two species. Instead, cheek scales and opercular spines were considered (Kottelat & Freyhof 2007). Fully scaled cheeks in *Z. streber* were reported by Kottelat (2007) and Ayache & Near (2009). Results from this study detected 4–6 scales only along the posterior lower edge of orbit but not under the central and anterior parts of the eye. Because of this, the cheeks of *Z. balcanicus* were placed in the category of partly scaled.

Table 1. Meristic characteristics in *Z. streber* and *Z. balcanicus* according different authors (including the present study).

	Z. streber	*Z. balcanicus*
D1	8–9 [1] 7–9 [2] 7–10 [3]	8 [6] 7–9 [7] 7–9 [3] 8 (present study)
D2	2–3/10–12 [1] 1/11–13 [2] 1–2/9–11 [3]	2/12–13[6] 2/8–10 [7] 2/10–12 [3] 1/14–15 (present study)
A	1–2/8–10 [1] 1/9–12 [2] 2/11–14 [4]	2/10–11 [6] 2/8–10 [7] 2/10 (present study)
L.l	73–78 [1] 70–83 [2] 70–85+4–7 [3]	80–82[6] 74–83 [7] 73–83+5–6 [3] 73–84+2–5 (present study)
L.l.a	4–7 [1] 5–6 [2]	5–7 (present study)
L.l.b	10–12 [1] 10–13[2]	12–15 (present study)
h.s	fully scaled [3] fully scaled [4]	2–6 [3] 4–6 (present study)
n.V	43–45 [2] 43–45 [5]	44–45 (present study)

Explanations: D1 – first dorsal fin; D2 – second dorsal fin; A – anal fin; L.l. – lateral line scales; L.l.a – scales above lateral line; L.l.b – scales below lateral line; Ch.s – cheek scales; nV – number of vertebrae; [1] Lusk (2004); [2] Simonovic (2006); [3] Kottelat & Freyhof (2007); [4] Ayache & Near (2009); [5] Collette (1963); [6] Karaman (1937); [7] Dimovski & Grupche (1971).

The presence of two spines on the opercular bone in *Z. balcanicus*, compared to one in *Z. streber* by Kottelat & Freyhof (2007), has attracted our interest to search for more details about osteological characters of *Z. balcanicus* to provide more useful anatomical data that could be of taxonomic value. Of course, the comparison with *Z. streber* is of great anatomical significance, but, unfortunately, data on osteological characteristics of *Z. streber* or other members of *Zingel* are rather scarce. There are only a few studies with partial descriptions of bony structures of *Z. streber* (Collette 1963; Wiley 1992; Kováč 2000; Bruner 2011). Namely, Collette (1963) mostly described fin architecture, and Wiley (1992) described 30 osteological characters to establish phylogenetic relationships within Percidae; Ayache & Near (2009) described 56, and Bruner (2011) 49. Kováč (2000) described ontogenetic sequences of skeletal structure during early development of *Z. streber*, not paying attention to their detailed anatomy.

Based on this scarce data in the literature, we found that most of the cranial and postcranial bones in *Z. balcanicus* follow the typical anatomical structure and shape assigned for the genus *Zingel.* Specifically for the cranium, the following are typical: the absence of the basisphenoid, orbitosphenoid, supramaxillary, and coronomeckelium; the lateral ethmoid articulates with the dorsal surface of the dorsal process of the first infraorbital; the supraoccipital crest is bilobed at the posterior end; the epioccipital process is present and moderate in size; seven infraorbitals are present; seven branchiostegal rays are present; the mandibular sensory canal has five enlarged sensory foramina; and the preopercular bone has serrate margins. For the postcranial skeleton, the following are common: lack of free predorsal pterygiophores; thin first anal proximal pterygiophore, about the same length as the second one; presence of three epiurals and five hypurals in the caudal complex; postero-dorsal margin of the supracleithrum and serrated post-temporal bones; and shape of the anterior process on the basipterygium is normal in length, while the medial process on the basipterygium is greatly reduced. However, it is necessary to note that few osteological characters (considered typical for genus *Zingel*) in some of the examined specimens of *Z. balcanicus* were found with different states. Thus, they were presented as the following: 1) three extrascapular bones instead of two; 2) the beginning of pleural ribs was from the second centrum instead of the third one; and 3) the first dorsal pterygiophore was located between fifth and sixth instead of the fourth and fifth neural spine. In order to show the stability of these osteological characters among *Z. balcanicus*, additional research is required.

Searching for stable taxonomic characters during this study, we emphasize that some specific osteological states are useful for distinguishing *Z. balcanicus* from the other species of *Zingel.* Specifically, the articular process of the premaxillary bone in all specimens of *Z. balcanicus* is almost square in shape, with height almost equal to width. This articular processes in *Z. streber* and *Z. zingel* are elongated to oval in shape, with height nearly 1.5 times greater than width (Ayache & Near 2009). Regarding teeth in the palatine bone, there are 12–18 located at the most anterior portion of the palatine bone in all specimens of *Z. balcanicus.* This is different from *Z. streber*, where palatine teeth are found along the entire anterior ramus of the palatine bone (Wiley 1992; Bruner 2011). On the other hand, Ayache & Near (2009) observed 18–39 teeth in both *Z. streber* and *Z. zingel* but with different dentigerous portions. As noted previously, the opercular spination is used as morpho-taxonomic characteristic between *Z. streber* and *Z. balcanicus* (Kottelat & Freyhof 2007). In this study, it has been confirmed that all examined samples from *Z. balcanicus* possess two well-developed spines on the postero-dorsal margins of the opercular bones. Furthermore, our results show that *Z. balcanicus* differs from both *Z. streber* and *Z. zingel* in the number of precaudal (=abdominal) centra. The vertebral column in *Z. balcanicus* is composed of 18–20 precaudal centra. Bruner (2011) counted 16–17 precaudal centra for *Z. streber* and 21–22 for *Z. zingel.* Moreover, until now, it was disputed whether the remnant (as a tube) of the canal of the supracleithral bone was present (Willey 1992; Ayache & Near 2009) or absent (Bruner 2011) in *Zingel* species. Our results show that in all specimens of *Z. balcanicus*, the supracleithral bone is without a canal.

During this study, some peculiar osteological characters in *Z. balcanicus* were revealed. Such osteological characters never before have been described for species of the genus *Zingel*, although their value was suggested in closely related genera by Wiley (1992), Ayache & Near (2009) and Bruner (2011). These osteological characters involve the hyomandibula, shape of the infraorbital bones, presence of "Spreitzer vertebrae", shape of gill rakers, and presence of an independent cartilage plate in the branchial basket.

Regarding the architecture of the hyomandibula, two osteological characters are present in *Z. balcanicus.* The first one is the presence of a spur between the opercular condyle and the antero-posterior corner of the hyomandibula, and the second is a sharp, vertical ridge that progresses down the posterior border of the hyomandibula, covering the anterior portion of the preopercle. Among Percidae, the presence of spurs was reported only for *Ammocrypta* and *Etheostoma* (Simons 1992), while the vertical ridge was found in some *Etheostoma* species (Norris 2001). Also, a detailed study of all examined specimens of *Z. balcanicus* revealed spine-like extensions on the ventral portions of the second and third infraorbital bones. Elsewhere in the genus *Zingel*, these types of spines are poorly known. Thus, further comparative studies among *Zingel* species are required.

As for the branchial basket osteology, it has been shown that all examined samples of *Z. balcanicus* possess gill rakers, which are shaped like hemispheres with small spines on the latero-ventral portions of ceratobranchials 1–4. Bruner (2011) reported that Romanichthyini (*Romanichthys* and *Zingel*) were the only percid genera found with this type of gill raker located on the first branchial arches, not specifying whether the rest of the arches possessed the same type of the gill rakers. Additionally, some of the examined specimens of *Z. balcanicus* possess an independent cartilage plate located between the uncinate process of epibranchial 1 and infrapharyngobranchial 2. Löffler et al. (2008) noted that an independent cartilage rod, named an interarcual, is also present in *Sander lucioperca* and in other members of Perciformes (Hilton et al. 2010). Unfortunately, as there are no osteological data regarding the architecture of the branchial basket in members of *Zingel*, we cannot make any comparisons to see if the other members possess an interarcual and tooth plate on epibranchial 3 and to determine presence of cartilage in infrapharyngobranchial 1.

Lastly, the results of this study show that in all of the examined specimens of *Z. balcanicus*, between the last precaudal vertebra connected with pleural and epineural ribs and the first caudal vertebra with a haemal spine, the presence of vertebrae with elongated, transverse processes without ribs was noticed. According to Bruner (2004), a vertebra with such characteristics should be named "Spreitzer vertebra". Within Percidae, this type of vertebra was noticed only in members of *Ammocrypta* (Bruner 2011). Additional research is needed to answer the question whether *Z. balcanicus* is unique within *Zingel* with respect to such osteological characters.

In this study, a complete osteological description for one member of the genus *Zingel* is established for the first time. The comparisons of osteological data with other members of *Zingel* (based on literature) showed enough stabile osteological characters and depicted new osteological criteria useful as characteristics for osteotaxonomic identification within *Zingel*. Given this osteological comparison, especially with *Z. streber*, the taxonomic distinction between species can be better distinguished. Furthermore, the results of this study made possible to propose new questions and scientific challenges in using osteological data as valuable markers in comparative studies not only for members of *Zingel* but also within Percidae.

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