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Regular paper

Dapalis pauciserratus, a new species of freshwater glassfishes (Teleostei, Ambassidae) from the Lower Oligocene of the Central Paratethys

by

Harald AHNELT* (1, 2), Katarina BRADIĆ-MILINOVIĆ (3) & Werner SCHWARZHANS (4)

Abstract. – We describe a new species of the fossil perciform genus *Dapalis* (Ambassidae), *Dapalis pauciserratus* n. sp., based on two articulated skeletons with otoliths in situ from the lower Oligocene of Raljin/Strelac, Babušnica basin, Southern Serbia. This species differs from congeners in the combination of following characters: (i) body elongate, fusiform; (ii) head triangular in shape; (iii) supraoccipital crest distinct; (iv) head without serrations except two large spine-like serrations on the corner of the preopercle; (v) premaxilla with a relatively narrow postmaxillary process located in the distal half; (vi) spines of the first and second dorsal fins, the anal fin and the pelvic fin strong but not massive; (vii) first spine of first dorsal fin long (42% of length of second spine); (viii) otoliths elongate (length/height = 1.4) with a narrow and elongate ostium, indistinct antirostrum, shallow excisura and an asymmetric and prominent rostrum.

Résumé. – *Dapalis pauciserratus*, une nouvelle espèce de poissons de verre d'eau douce (Teleostei, Ambassidae) de l'Oligocène inférieur de la Paratéthys Central.

Nous décrivons une nouvelle espèce du genre perciforme fossile *Dapalis* (Ambassidae), *Dapalis pauciserratus* n. sp., basée sur deux squelettes articulés avec des otolithes in situ provenant de l'Oligocène précoce de Raljin/Strelac, bassin de Babušnica, Serbie méridionale. Cette espèce diffère de ses congénères par la combinaison des caractères suivants : (i) corps allongé, fusiforme ; (ii) tête de forme triangulaire ; (iii) crête supraoccipitale distincte ; (iv) tête sans dentelures à l'exception de deux grandes dentelures en forme d'épines sur le coin du préopercule ; (v) prémaxillaire avec un processus postmaxillaire relativement étroit situé dans la moitié distale ; (vi) épines de la première et de la deuxième nageoire dorsale, de la nageoire anale et de la nageoire pelvienne fortes mais non massives ; (vii) première épine de la première nageoire dorsale longue (42% de la longueur de la deuxième épine) ; (viii) otolithes allongés (longueur/hauteur = 1,4) avec un ostium étroit et allongé, un antirostrum indistinct, une excisura peu profonde et un rostrum asymétrique et proéminent.

INTRODUCTION

Dapalis Gistel 1848 is an extinct genus of the glass perch family Ambassidae Klunzinger, 1870 (formerly Chandidae Fowler, 1905) and existed from the Middle Eocene to the Middle Miocene (Reichenbacher, 1988). Species of this genus first appeared in Europe in the Middle and Late Eocene when freshwater habitats were island-bound with few primary freshwater fishes (Popov *et al*., 2001). During this period a high number of marine immigrants adapted to freshwater including Ambassidae (summarized in Popov *et al*., 2001) like *Dapalis hungaricus* (Schubert, 1912) and *Dapalis ventricosus* Nolf & Reichenbacher, 1999. This trend of marine species to occupy limnic and brackish waters continued in the Lower Oligocene (Rupelian) and was also documented for the ambassid genus *Dapalis* (summarized in Popov *et al*., 2002), which diversified in a series of species like the brack-ish *Dapalis macrurus* (Agassiz, 1836), the brackish to fresh-water *Dapalis angustus* Reichenbacher & Weidmann, 1992 and *Dapalis transylvanicus* Reichenbacher & Codrea, 1999 and the limnic *Dapalis borkensis* (Weiler, 1961) known from freshwater deposits (Table I). This diversification of *Dapalis* in brackish waters and in freshwaters of Europe continued throughout the entire Oligocene and the late Early Miocene (Ottnangian), when *Dapalis* seemingly got extinct (Reichen-bacher, 1998).

The majority of formally described species of *Dapalis* of Europe (Table I) is only documented from otoliths (*e.g*., Weiler, 1966; Brzobohatý, 1969; Stinton and Kissling, 1968; Reichenbacher, 1988, 1993; Reichenbacher and Weidmann, 1992; Reichenbacher and Codrea, 1999). Species descriptions based on more or less well-preserved skeletons are rare (Agassiz, 1833-1843; Meyer, 1852; Weiler, 1955; Gaudant, 2007; Gaudant *et al*., 2018) as are descriptions of specimens

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(1) First Zoological Department, Natural History Museum of Vienna, Burgring 7, 1010 Vienna, Austria. harald.ahnelt@nhm-wien.ac.at
(2) Department of Evolutionary Biology, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria. harald.ahnelt@univie.ac.at
(3) Geological Survey Serbia, Rovinjska 12, 11000 Belgrade, Serbia. katarina.bradicmilinovic@gzs.gov.rs
(4) Natural History Museum of Denmark, Zoological Museum, Universitetsparken 15, 2100 Copenhagen, Denmark. wwschwarz@aol.com
* Corresponding author

Table I. – Species of the genus *Dapalis* from the Eocene, Oligocene and Miocene in Europe. Species from the Oligocene are shaded in grey; the new species is shown in bold. The otoliths of the Early Oligocene species are compared with the otoliths of *D. pauciserratus* n. sp. in detail (see text). bra – brackish water, fre – fresh water. MP, MN – mammal zones. O =, otolith; S = skeleton. [1] Reichenbacher (1999), [2] Reichenbacher *et al.* (2004), [3] Pirkenseer *et al.* (2013), [4] Reichenbacher and Codrea (1999), [5] Reichenbacher *et al.* (2013), [6] Reichenbacher (1988), [7] Reichenbacher and Weidmann (1992), [8] Reichenbacher (1993), [9] Martini (1983), [10] Gaudant *et al.* (2018), [11] Schultz (2000), [12] Gaudant (2013), [13] Bránkin *et al.* (1983), [14] Reichenbacher and Cappetta (1999), [15] Weinfurter (1967), [16] Nolf and Reichenbacher (1999), [17] van Hinsbergh (1980), [18] Gaudant (2007), [19] Weiler (1966), [20] Brzobohatý (1969), [21] Reichenbacher (2000), [22] Weiler (1963).

	Facies	Chronostratigraphy	Biostratigraphic Correlation	Otolith/skeleton based
D. kühni [15]	fre–bra	Middle Miocene, Badenian	MN 5–MN 6	O
D. formosus [1,5,6,8,9,19,20]	bra	Early Miocene, Eggenburgian, Ottnangian	MN 2–MN 4	O/S
D. crassirostris [8,19,20]	fre–bra	Early Miocene, Ottnangian	MN 4	O
D. curvirostris [7,8,9,19,20]	bra	Early Miocene, Eggenburgian, Ottnangian	MN 2–MN 4	O
D. kaelini [8]	bra	Early Miocene, Eggenburgian, Ottnangian	MN 2–MN 4	O
D. rhenanus [14,17,21,22]	bra	Early Miocene, Aquitanian	MN 2	O
D. carinatus [7]	fre–bra	Late Oligocene – Early Miocene	MP 28–29, MN 1	O
D. minutus [10,11]	fre–bra	Late Oligocene – Early Miocene	MP 26–MN 2	S
D. rhomboidalis [7]	fre–bra	Late Oligocene – Early Miocene	MP 28–MN 1	O
D. transylvanicus [4]	fre–bra	Early Oligocene, Rupelian	MP 24	O
D. borkensis [4]	fre	Early Oligocene, Rupelian	MP 24	O
D. pauciserratus n. sp.	**fre**	**Early Oligocene, Rupelian**	**MP 23**	**O/S**
D. angustus [1,2,3,4,7]	fre–bra	Early Oligocene, Rupelian	MP 21–MP 23	O
D. macrurus [11,12,13]	bra	Early – Late Oligocene	MP 21–MP30	O/S
D. ventricosus [16]	bra	Middle Eocene, Late Lutetian – Early Bartonian	MP 13–MP 14	O
D. praecursor [18]	fre	Middle Eocene, Late Lutetian	MP 13–MP 14	O/S
D. hungaricus [16]	bra	Middle Eocene, Late Lutetian, Early Bartonian	MP 12–MP 13	O

with otoliths *in situ* (Weiler, 1939, 1955). Only few species of the genus *Dapalis* (formerly *Smerdis* Agassiz, 1833; preoccupied by *Smerdis* Leach, 1817 in Crustaceans) are known from articulated skeletons, *e.g.*, *Dapalis macrurus* [Early-Late Oligocene (Bránkin *et al.*, 1983; Gaudant, 1992, 2013)], *Dapalis minutus* [Late Oligocene (Gaudant *et al.*, 2018)] and *Dapalis formosus* [Early Miocene (Meyer, 1852; Martini, 1983; Weiler, 1955; Reichenbacher, 1999)].

In his famous book *Recherches sur les Poissons Fossiles*, Louis Agassiz (1833-1843: Vol. 4, Table 8, figs 1-8) described, besides *Dapalis minutus* and *Dapalis macrurus*, four species (as *Smerdis*) based on skeletons, *Smerdis latior*, *Smerdis micracanthus*, *Smerdis pygmaeus* and *Smerdis ventralis*. But a nearly continuous dorsal fin (clearly separated two fins in *Dapalis*) and the third spine of the first dorsal fin longest (second spine of the first dorsal fin longest in *Dapalis*) separates *Smerdis micracanthus* and *Smerdis pygmaeus* from *Dapalis* and from Ambassidae in general. The taxonomic status of the two other species, *Smerdis ventralis* and *Smerdis latior*, is difficult to assess from the description and from the figures because important diagnostic features like

the dorsal fins (*Smerdis ventralis*) or large parts of the head (*Smerdis latior*) are missing. Apparently, the genus *Dapalis* needs revision, especially the species described by Agassiz (1833-1843).

Many so-called *Dapalis* species which were described from skeletons as *Smerdis* are now placed with other generic names in various fish families like *e.g.*, *Smerdis budensis* Heckel, 1856 in Percoidei *incertae sedis* (Bieńkowska-Wasiluk and Paldyna, 2018), *Smerdis isabellae* Gaudry, 1862 in Moronidae (Argyriou, 2022), *Smerdis krambergeri* Anđelković, 1984 in Mugilidae (Gaudant, 1998), *Smerdis rotundus* Weiler, 1963 in Atherinidae (Reichenbacher, 1993) and *Smerdis sieblosensis* Winkler, 1880 in the genus *Dapaloides* of the "Percichthyidae" (Gaudant, 1985; Reichenbacher, 1993, 1995). *Smerdis micracanthus* Agassiz, 1835 was placed in Centropomidae (Schultz, 2000).

Various outcrops with fish-remains, including *Dapalis*, were described in the second half of the 20th century from Serbia (summarized in Anđelković, 1989). The Koritnica-Babušnica basin in southeast Serbia is well-studied (*e.g.*, Petcović, 1930; Pantić, 1956; Anđelković, 1970, 1978, 1989;
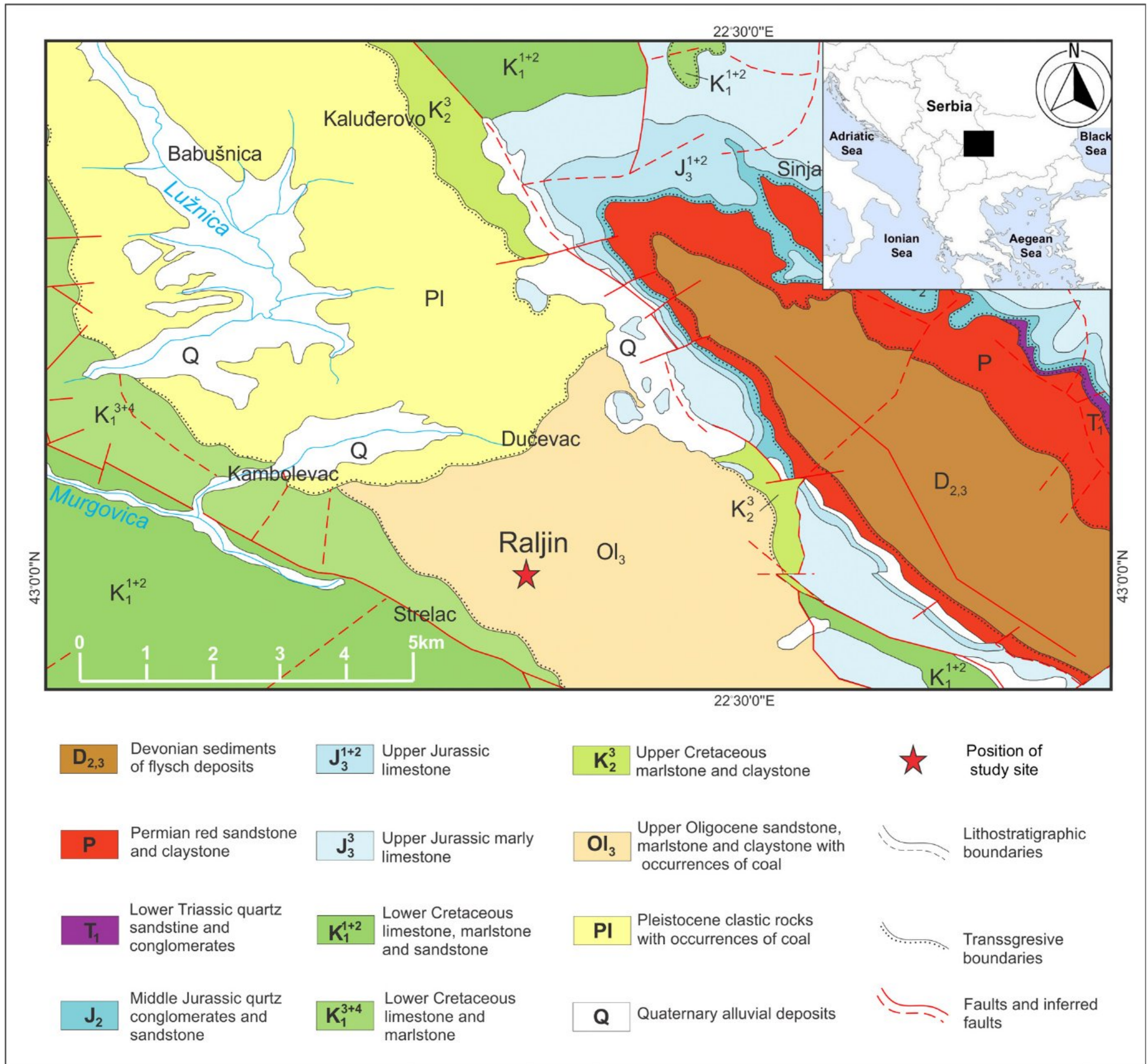
Figure 1. – Location and stratigraphy. Simplified geological map of the Babušnica basin, modified after (Dimitrijević *et al.*, 1973, 1977, 1980), with the position of the study site marked as red star.

Bruijn *et al.*, 2018; Wessels *et al.*, 2020; Weerd *et al.*, 2022). These deposits were variously dated from the Lower Oligocene to the Lower Miocene (summarized in Anđelković, 1989; Gaudant, 1998). However, recent mammalian records from the localities Raljin/Strelac of the Babušnica basin showed a Lower Oligocene (Rupelian) age of the lacustrine sediments in this region (Bruijn *et al.*, 2018; Weerd *et al.*, 2022).

Anđelković (1989) reported three species of *Dapalis* (as *Smerdis*) from the Tertiary of Serbia from three locations in the Babušnica Basin (Stol, Brataševac and Dučevac), *Dapal-is macrurus*, *Dapalis minutus* and *Dapalis formosus*. Nevertheless, all these specimens were misidentified and are actually remains of gobiid and mugilid fish species respectively (*Dapalis macrurus* and *Dapalis formosus*) or of a mugilid species (*Dapalis minutus*) (Gaudant, 1998; Schultz, 2000; Bradić-Milinović *et al.*, 2019). Recently, the Geological Survey of Serbia (GZS) in Belgrade (Serbia) obtained two articulated specimens of the genus *Dapalis* with otoliths in situ from freshwater deposits at Raljin close to the village Strelac in southeastern Serbia. The stratigraphic position of these sediments was determined as early Oligocene age (Rupelian)

on the bases of vertebrate remains, of fishes (Anđelković, 1970, 1978, 1989) and of micromammals (Bruijn *et al.*, 2018; Marković *et al.*, 2020; Weerd *et al.*, 2022). From this locality no fossil fishes have previously been recorded. These finds are also remarkable for representing the first record of skeletons with otolith in situ from the area. Here we describe these specimens as a new species of *Dapalis* from the Lower Oligocene of Serbia.

MATERIALS AND METHODS

Two articulated skeletons with otoliths *in situ* were collected by Mr. Žarko Petrović near the site "Raljin" (43°01'10"N, 22°29'30"E), close to the village Strelac, Babusniča basin, Serbia. The fishes were embedded in lacustrine marlstone. The specimens are housed in the Geološki Zavod Srbije (Geological Survey of Serbia) (GZS), Belgrade, Serbia, as part of paleontological collection and were catalogued as GZS-RA1 and GZS-RA5.

Regional geology and locality
Geological setting

The Babušnica basin, a relative narrow and elongated basin, is part of the tectonic unit of the Carpatho-Balkanides (Fig. 1). It is about 520 km long, and extends along a fault zone NW-SE (Ridan-Krepoljin dislocation) oriented and is located in southeastern Serbia between Koritnica and Babušnica (Anđelković *et al.*, 1988; Anđelković, 1989; Marović *et al.*, 2007; Bruijn *et al.*, 2018). This basin is connected with the Koritnica Basin, and towards the southeast it extends to the Jerma valley into Bulgaria, which in turn is connected with the Sturma fault zone (Zagorchev, 2001). The following tectonic sequence is recognized: 1) formation of grabens of Eocene to Oligocene age, 2) subvulcanic intrusions and dykes, 32-29 Ma, 3) formation of coal-bearing basin during the Late Oligocene-Early Miocene, 4) extensional tectonic during the Middle Miocene (Zagorchev, 2001).

Stratigraphic setting

The lacustrine sediments in the Babušnica Basin directly overly Upper Cretaceous sediments. The Cenozoic sedimentation of the Babušnica Basin is divided in two series. First, a lower level of sedimentation represented by red conglomerate and sand with large grains up to 50 cm. Following this initial phase of sedimentation, the basin subsided and became subject to lake deposits consisting of grey marlstone, sandstone and marly limestone, which constitutes the upper series of Babušnica Basin. The final phase of sedimentation in the basin is marked by claystone with fossil fishes and paleoflora. This last sedimentary phase shows common intercalation of tuff (Anđelković *et al.*, 1988).
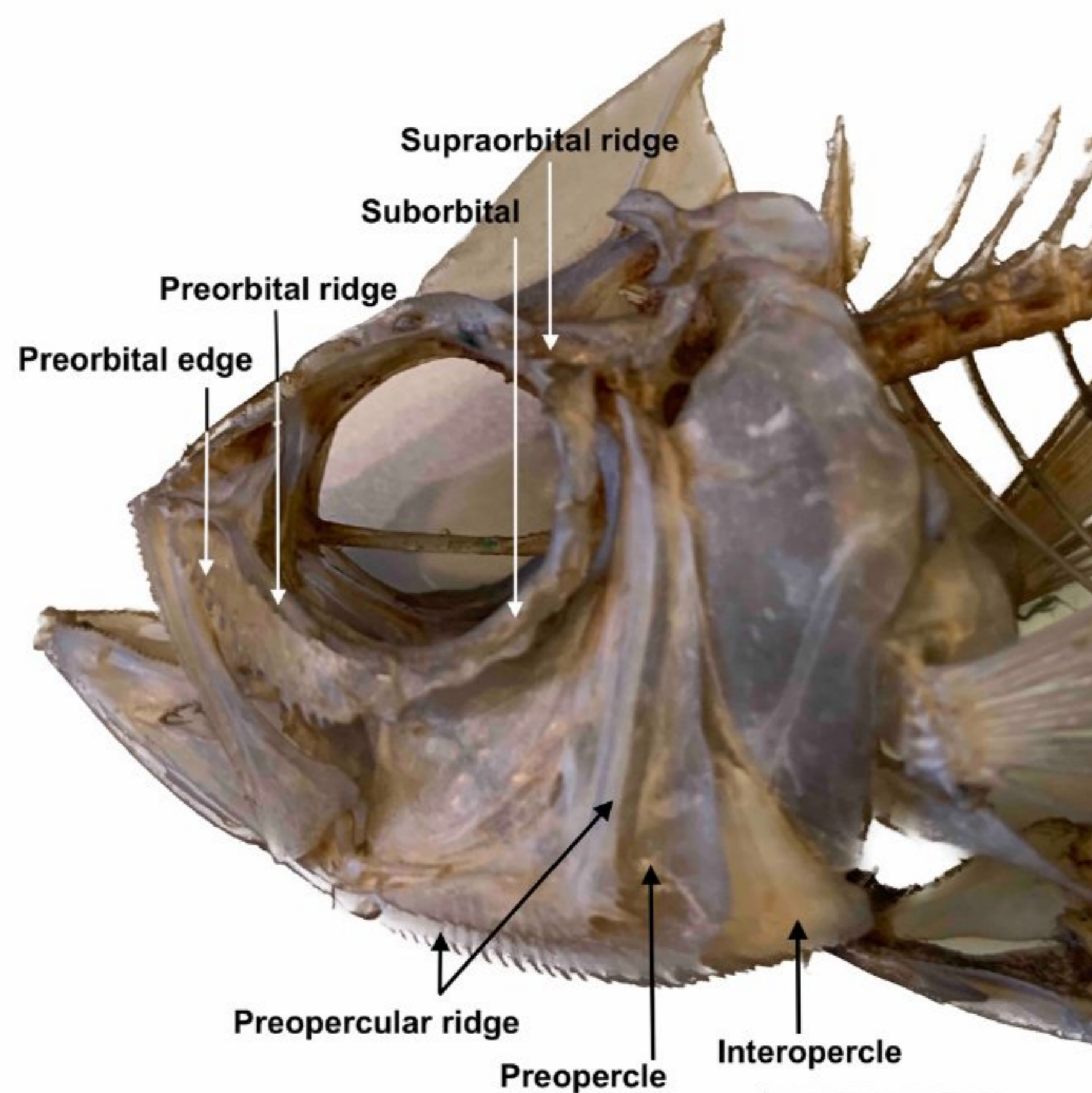

Figure 2. – Head of *Ambassis ambassis* (NMW 93975) showing ridges and edges of taxonomic importance. Nomenclature after Fraser-Brunner (1954). Scale bar is 10 mm.

Palaeontological investigations in the area have been rather few. Based on fish remains, the last sedimentation phase in the Babušnica Basin was interpreted to be of Early Oligocene, Rupelian age (Anđelković, 1970, 1978, 1989). An evaluation of the paleoflora of the Babušnica Basin gave conflicting age estimates, *e.g.*, Oligocene (Pantić, 1956), Early Oligocene (Mihajlović, 1985) and Oligo-Miocene (Petcović, 1930). Micromammal remains from the locality Raljin was identified to be of Early Oligocene age (Bruijn *et al.*, 2018; Marković *et al.*, 2020; Weerd *et al.*, 2022).

Serration of cephalic bones

In Ambassid fishes the serrations of opercular, suborbital (infraorbital) and supraorbital bones are of taxonomic importance (Fraser-Brunner, 1954; Martin and Heemstra, 1988). Various names are used in literature for the first infraorbital bone, *e.g.*, lachrymal, preorbital or suborbital. "Preorbital" has been used frequently in the taxonomy of Ambassidae and is continued here as "preorbital ridge" and "preorbital edge" (Fig. 2).

Comparative skeletal material
Dapalis formosus (Meyer, 1852): SMNS 002960; Unterkirchberg, Deutschland.
Dapalis macrurus (Agassiz, 1834): NHMW 2413; Aiguebelle près Aubenas-les-Alpes, France. SMNS 55544, Céreste, Alpes de Haute, France.

Dapalis minutus (Agassiz, 1834): NHMUK P76287, NHMW 2398, NHMW 2399, NHMW 2403 and MNHN Aix-243 (photography); Aix-en-Provence, France.

Comparison of *Dapalis* otoliths from the Oligocene based on the descriptions in the literature

Dapalis angustus from Reichenbacher and Weidmann (1992), Reichenbacher and Codrea (1999), Pirkenseer *et al.* (2013).

Dapalis borkensis from Weiler (1961), Reichenbacher (1995).

Dapalis carinatus from Stinton and Kissling (1968), Reichenbacher and Weidmann (1992), Reichenbacher and Codrea (1999).

Dapalis macrurus from Weiler (1939), Martini (1965).

Dapalis rhomboidalis from Stinton and Kissling (1968), Reichenbacher and Weidmann (1992), Reichenbacher and Codrea (1999).

Dapalis transylvanicus from Reichenbacher and Codrea (1999).

Apogonidae with compartmentalized dorsal and anal fin spines, from photographs of cleared and stained specimens

Ambassis agrammus Günther, 1867, US 173828
Ambassis buruensis Bleeker, 1856, UF 237575
Ambassis dussumieri Cuvier, 1828, IE 16526
Ambassis macleayi (Castelnau, 1878), US 173817
Denariusa australis (Steindachner, 1867), US 173814
Gymnochanda ploegi Tan & Lim, 2014, IE 15773
Parambassis baculis (Hamilton, 1892), UF 178036
Parambassis lala (Hamilton, 1822), IE 11182
Parambassis piratica (Roberst, 1989), UF 166901
Parambassis siamensis (Fowler, 1937), IE 15611

Abbreviation of collections

IE, Deutsches Meeresmuseum, Stralsund; MNHN, Muséum national d'Histoire naturelle, Paris; NHMW, NHMUK, Natural History Museum, London; Naturhistorisches Museum Wien; UF, Florida Museum of Natural History, Gainesville; US, National Museum of Natural History, Washington.

RESULTS

Class Actinopterygii *sensu* Goodrich, 1930
Subclass Neopterygii Regan, 1923
Infraclass Teleostei Müller, 1845
Division Acanthopterygii Cope, 1871
Clade Percomorpha Cope, 1871
Family Ambassidae Klunzinger, 1870
Genus *Dapalis* Gistl, 1848

Dapalis pauciserratus **nov. spec.** (Figs 3-5)
Holotype. Register number GZS-RA1, 38.8 mm SL; Raljin, Babušnica Basin, Serbia; leg. Žarko Petrović.
Paratype. Register number GZS-RA5, 26.6 mm length of fish (last 3 vertebra and caudal fin missing); Raljin, Babušnica Basin, Serbia; leg. Žarko Petrović.

Etymology

The new species is named *pauciserratus* (Latin: having few serrations) with reference to the preopercle, which has distinctly fewer serrations than the preopercle of the other congenerics.

Diagnosis

An ambassid fish of small size (42 mm SL); 24 (10 + 14) vertebrae; first dorsal fin with seven spines; first spine much shorter than the second; second dorsal fin with a single spine and nine rays; anal fin with three spines, each supported by a pterygiophore; spines with compartmentalized internal structure; pterygiophore of second spine very long and in close contact with the haemal spine of the first caudal vertebra; first spine of first dorsal fin (42.6% in length of second dorsal spine) and of anal fin (69.8% in length of second anal fin spine respectively) relatively long; body shape elongate, slender with a narrow head (23.9 % of SL) and body (24.1% in SL); orbit large (36.2 % of head length); mouth terminal, slightly oblique in position; few serrations on head, only present on corner of preopercle; otolith length to height = 1.3.

Description

Counts and measurements are reported in Table II and Table III.

The skeletons of both specimens are incompletely preserved. The bones of the head are only partly discernible (Figs 3-4).

Neurocranium

The skull is large and massive. Its dorsal and occipital regions are badly damaged. The dorsal and partly the posterior limits of the orbit are formed by the frontal, the posteroventral part by the sphenotic. The parasphenoid is long. The supraoccipital is distinctly elevated.

Circumorbitalia (Suborbitalia + Supraorbitalia)

Lacrimal (infraorbital bone 1, preorbital) is oval, elongated, laminar and large; it extends ventrally to the anterior rim of the orbit; its ventral rim is smooth and not serrated; the suborbitals (infraorbitals) form a narrow band along the ventral edge of the orbit and are not serrated; no serrations were found on the supraorbital bones.

Table II. – Body proportions in % standard length of *Dapalis pauciserratus* n. sp. and *Dapalis minutus* from the type locality Aix-en-Provence, and *Dapalis macrurus* from Aiguebelle près Aubenas-les-Alpes and Céreste. Values are mean and, in parentheses, range. D1I and DII length, length of the first and second spine of the first dorsal fin, AI and AII length, length of the first and second spine of the anal fin. *Dapalis minutus*: NHMW 2398, NHMW 2399, NHMW 2403; *Dapalis macrurus*: SMNS 55544, NHMW 2413. Asterisk = values are from two specimens. Distinct differences (> 5%) between *Dapalis pauciserratus* n. sp. and *Dapalis minutus* and *Dapalis macrurus* are highlighted in grey.

	D. pauciserratus	*D. pauciserratus*	*D. minutus*	*D. macrurus*
	Holotype (RA1)	Paratype (RA5)	(n = 3)	(n = 3)
SL (mm)	42.0	–	43.3 (41.5-44.9)	62.7 (56.2-66.6)
% SL				
Predorsal length	41.2	–	48.7 (48.4-48.9)	43.4 (42.5-44.1)
Preanal length	66.0	–	68.2 (67.7-68.8)	68.3 (66.2-69.4)
Tail length	36.3	–	37.2 (36.1-38.2)	36.9 (34.8-38.9)
Head length	31.4	–	30.5 (30.4-30.8)	32.4 (30.9-34.1)
Head depth	23.9	–	27.8 (27.6–28.1)	27.9 (26.5-30.5)
Snout length	7.8	–	7.5 (7.3-7.6)	9.5 (9.4-9.5)
Orbit diameter	11.8	–	11.4 (11.2-11.6)	9.5 (9.2-9.8)
Postorbital length	13.4	–	11.8 (11.6–11.9)	12.8 (11.8-14.9)
Cheek depth	7.2	–	10.6 (10.1-10.9)	8.6 (7.6-9.7)
Body depth	24.2	–	35.9 (34.9-37.1)	29.3 (28.6-30.6)
Caudal peduncle length	24.2	–	23.4 (23.2–23.7)	23.8 (22.7-24.4)
First dorsal-fin base	14.4	–	16.2 (15.7-16.8)	13.9 (12.9-14.6)
D1I length	5.2	–	5.9 (5.5-6.3)	5.4 5.16.0)
D1II length	damaged	–	31.1 (28.9–31.8)	19.7 (18.8-20.8)
AI length	8.1	–	5.7 (5.6–5.8) *	5.0 (4.0-5.9) *
AII length	12.1	–	22.0 (21.7-22.3) *	15.4 (14.1-16.6)
% Head length				
Head depth	77.0	78.3	90.2 (89.8-90.7)	86.0 (82.8-89.4)
Snout length	23.7	21.7	23.8 (23.6-23.9)	29.2 (27.7-30.6)
Orbit diameter	35.4	36.9	36.2 (35.8-36.4)	29.6 (27.7-30.6)
Postorbital length	42.6	41.3	38.2 (37.9-38.6)	39.3 (36.6-43.7)
Cheek depth	23.0	26.1	34.5 (33.9-34.8)	26.6 (24.7-28.4)
First dorsal-fin base	45.9	45.7	52.9 (52.4-53.1)	43.0 (40.2-45.9)
% D1II				
D1I	–	42.6	18.6 (17.9-19.8)	27.2 (25.9-28.8)
% AII				
AI	69.4	70.1	26.3 (25.9-26.7) *	30.4 (25.6-35.2) *

Jaws

Premaxilla and maxilla of the upper jaw are slender, relative to the bones of the lower jaw. The premaxilla carries three processes, a narrow ascending process followed by a large, roundish articulating process; both processes are separated by a narrow gap; at about the middle of the premaxilla rises the narrow, triangular postmaxillary process; no teeth are visible on the premaxilla of RA1 but small, hardly visible, conical teeth are developed on the premaxilla of RA5. The maxilla is rod-shaped and straight except for its most anterior part; this part is forked in two processes and bent anteriorly; the median process is slightly longer than the lateral process and contacts the maxillary process of the palatine; the lateral process contacts the articular process of the premaxilla; posteriorly, the maxilla widens ending in a wide triangular plate with straight edge.
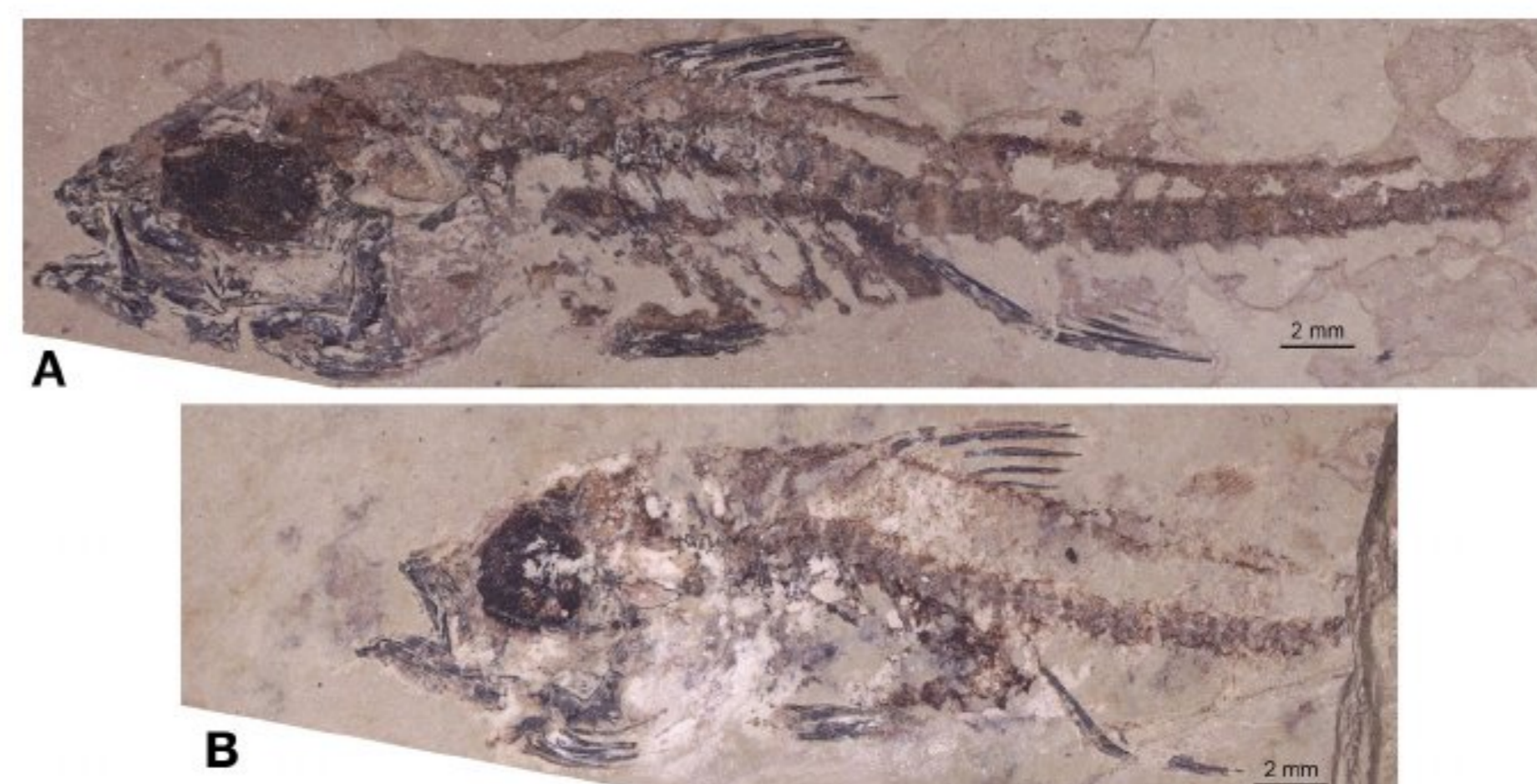

Figure 3. – Articulated skeletons of *Dapalis pauciserratus* n. sp. **A**: Holotype (GZS-RA1); **B**: Paratype (GZS-RA5).

Table III. – Meristic information for *Dapalis pauciserratus* n. sp., and *Dapalis minutus* from the its type locality Aix-en-Provence, and *Dapalis macrurus* from Aiguebelle près Aubenas-les-Alpes and Céreste. Differences between *Dapalis pauciserratus* and *Dapalis minutus*, *Dapalis macrurus* are highlighted in grey. *Dapalis minutus*: NHMW 2398, NHMW 2399, NHMW 2403, MNHN Aix 243; *Dapalis macrurus*: SMNS 55544, NHMW 2413.

|	*D. pauciserratus*	*D. pauciserratus*	*D. minutus*	*D. macrurus*
	Holotype	Paratype (n = 1)	n = 4	n = 3
SL (mm)	42.0	–	43.3	62.7
First dorsal-fin	VII	VII	VII–VIII	VII
Second dorsal-fin	I/6+	I/?	I/9–10	I/10
Anal-fin	III/?	III/?	III/8	III/7
Pectoral-fin	–	–	12+–15?	15
Pelvic-fin	I/5	I/5	I/5	I/5
Caudal fin (d/v)	missing	missing	17 (9/8)	17 (9/8)
Vertebra	24	–	24	24
Precaudal vertebra	10	10	10	10
Caudal vertebra	14	–	14	14
Supraneuralia	?	?	3	3
Preopercle	2 (3?) serrations	2 (3?) serrations	serrations numerous	serrations numerous
Preopercular ridge	smooth	smooth	smooth	smooth
Preorbital ridge	smooth	smooth	smooth	serrations
Preorbital edge	smooth	smooth	serrations	?
Suborbital	smooth	smooth	serrations	smooth
Interopercle	smooth	?	serrations	?
Supraorbital ridge	smooth	smooth	smooth	?
Teeth premaxilla	small, conical	small, conical	small, conical	?
Teeth dentary	small, conical	small, conical	small, conical	?
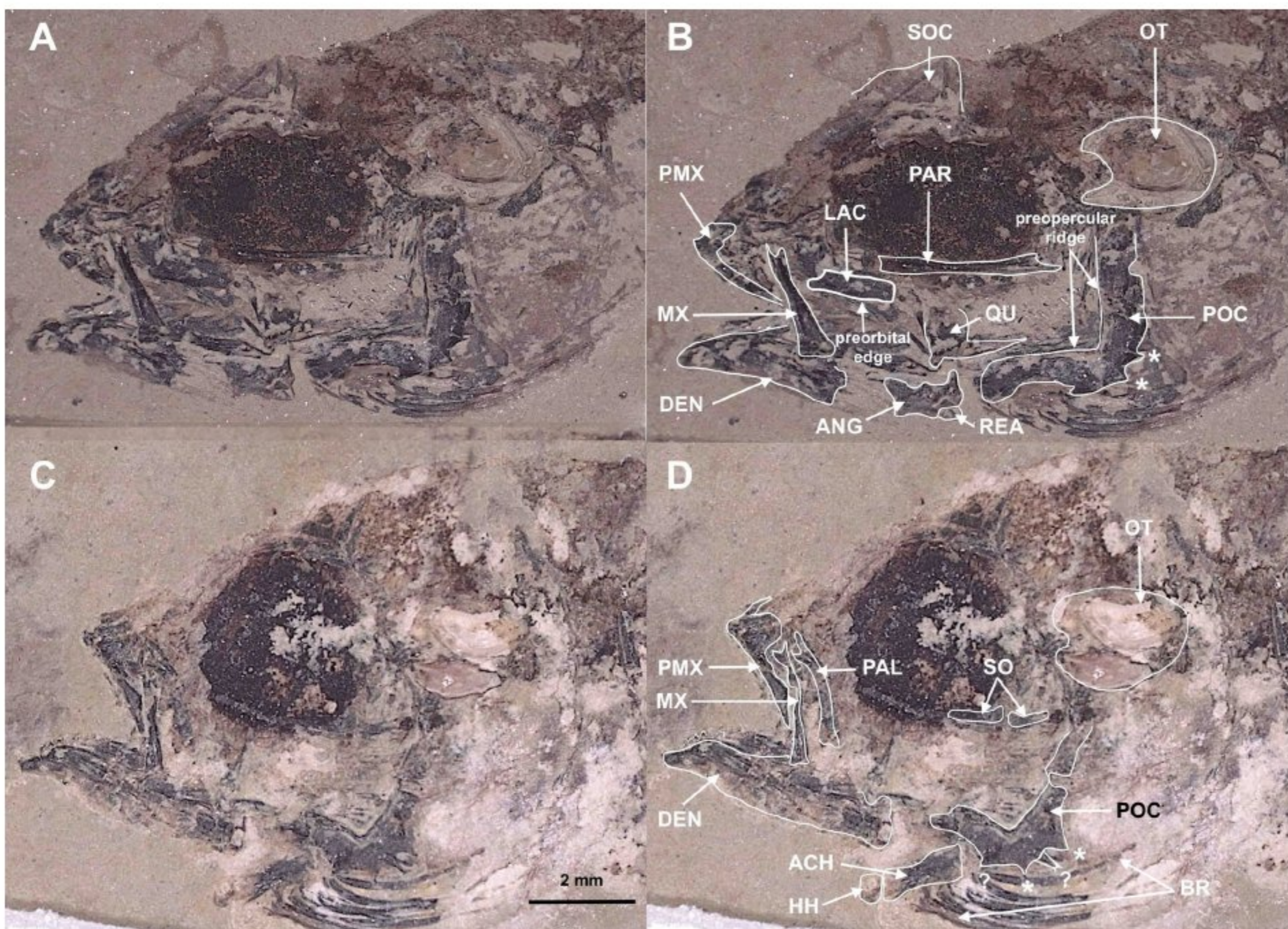
Figure 4. – Heads of *Dapalis pauciserratus* n. sp. **A**: Holotype (GZS-RA1); **B**: Paratype (GZS-RA5). ACH, anterior ceratohyale; ANG, angulo-articulare; BR, branchiostegal rays; DEN, dentary; HH, hypohyale; MX, maxilla; OP, opercle; OT, otolith; PMX, premaxilla; PAL, palatine; PAS, parasphenoid; POC, preopercle; QU, quadrate; REA, retro-articulare; SO, suborbitals (infraorbitalias); SOC, supraoccipitale. * spine-like serrations at corner of preopercle; ?, a possibly third spine-like serration (see text for explanation).

The bones of the lower jaw are relative massive and the dentary and the anguloarticulare are rather large; the suture between these two bones and the shape of the coronoid process are not visible; small, conical teeth are present on the dentary (paratype); the retroarticular is positioned ventrally to the ventro-posterior corner of the anguloarticular slightly exceeding it caudally and ending in a rounded tip; at this tip attaches the interoperculo-mandibular ligament (LIM) which

connects the lower jaw to the opercular series.

Suspensorium

The quadrate consists of a large laminar anterior plate and ventral of a caudally directed massive preopercular process; this process is in a close contact with the dorsal edge of the horizontal arm of the preopercle; the articular process of the quadrate is relatively small and antero-ventrally directed. The palatine is massive, like the maxillary its anterior most part is bent anteriorly; it is also forked with two processes; the ethmoid process is massive and long and directed medio-dorsally; it connects the palatine with the lateral ethmoid of the neurocranium; the smaller and more slender maxillary process, is directed anterolateral and connects with the lateral process of the maxilla (RA5).

Opercular series

Opercle, subopercle and interopercle are not recognizable. The preopercle is reverted L-shaped and consists of a posterior vertical limb and an anterior horizontal limb; these two limbs are positioned rectangular to each other; the preopercle is relatively complete, with a part of the ventral margin of the horizontal limb missing in both specimens; the posterior margin of the vertical limb is complete in the holotype but is partly missing in the paratype; this margin is smooth except for two short spine-like serrations at the corner where both limbs meet (complete in both specimens); each of these spines has a wide base, is short, equilateral triangular and pointed; the preopercular ridge is smooth. There is possibly a third spine ventrally on the preopercle of the paratype. Exactly at this position where the ventral margin of the preopercle is broken off.

Hyoid bar

The hyoid bar is partially preserved in the paratype. The anterior ceratohyal is club-shaped, the hypohyals are bulbous. There are five branchiostegal rays, the two anteriormost thin, the following three saber-like.

Axial skeleton

The vertebral column comprises 24 vertebrae, 10 abdominal (precaudal) and 14 caudal, including the urostyle (compound centre) (RA1); the abdominal portion is long, 77% of the caudal portion; the vertebral centres are just somewhat longer than height; the neural spines are narrow and hardly discernible, emerging from the anterior part of the centra, subsequently shifting posteriorly from caudal vertebra 7 on (RA1); the posterior most neural spines are not discernible, which is also the case for the haemal spines; from these just the first is visible, and from the bases of the haemal spines 6-10; like the neural spines also the haemal spines are positioned more posteriorly beginning with caudal vertebra 7.

Eight pairs of long pleural ribs extend from the vertebrae 3-10.

Caudal skeleton

The caudal skeleton is completely missing in the paratype and nearly completely missing in the holotype. In latter, the parhypural and the two hypural plates, the ventral plate (formed by the fused hypurals 1+2) and the dorsal plate (formed by the hypurals 3+4), are discernible, both in close contact with the urostyle (compound centre).

Median fins

There are two dorsal fins, both distinctly separated. The first (D1) is composed of seven spines, the second (D2) of one spine and of soft rays. D1 originates dorsal to the 4th vertebra; the seven spines are moderately strong and acute; each spine is associated with one pterygiophore; the first spine is short (38.8% of the length of the second spine), the seventh is slightly shorter than the first and therefore the shortest in this series (34.5% of the length of the second spine); the first three spines are the strongest and are supported by long, strong pterygiophores; the compartmentalized internal structure, seemingly characteristic for Ambassidae, is recognizable on the third spine of the first dorsal fin of the holotype. No supraneurals (predorsal bones) are discernible; the first pterygiophore inserts in the interneural space between the neural spines (NS)1 and NS2, the second and the third pterygiophore insert in the interneural space between NS2 and NS3.

The anal fin originates ventral to the 3rd caudal vertebra. Three spines precede the soft part of this fin; the first spine is short, the second the longest and the third somewhat shorter than the second; the spines are moderately strong and acute; the pterygiophores of the first two spines are very long and strong, of equal length and strength; distally they are somewhat wider, proximally they end in a narrow tip; both pterygiophores lie close together and form this way a long, narrow club-shaped structure; the third pterygiophore, hardly to discern, is seemingly distinctly shorter than the second; the first two pterygiophores are prehaemal pterygiophores which insert immediately anterior to the first haemal spine; the first three pterygiophores are strongly inclined posteriorly.

Paired fins and girdles

Pectoral fins and the bones of the pectoral and pelvic girdles are not discernible. The pelvic fins are short and end below a vertical through the base of the third D1 spine; they are each composed of a spine and five soft rays; the spine is moderately strong and shorter than the fin rays.

Caudal fin

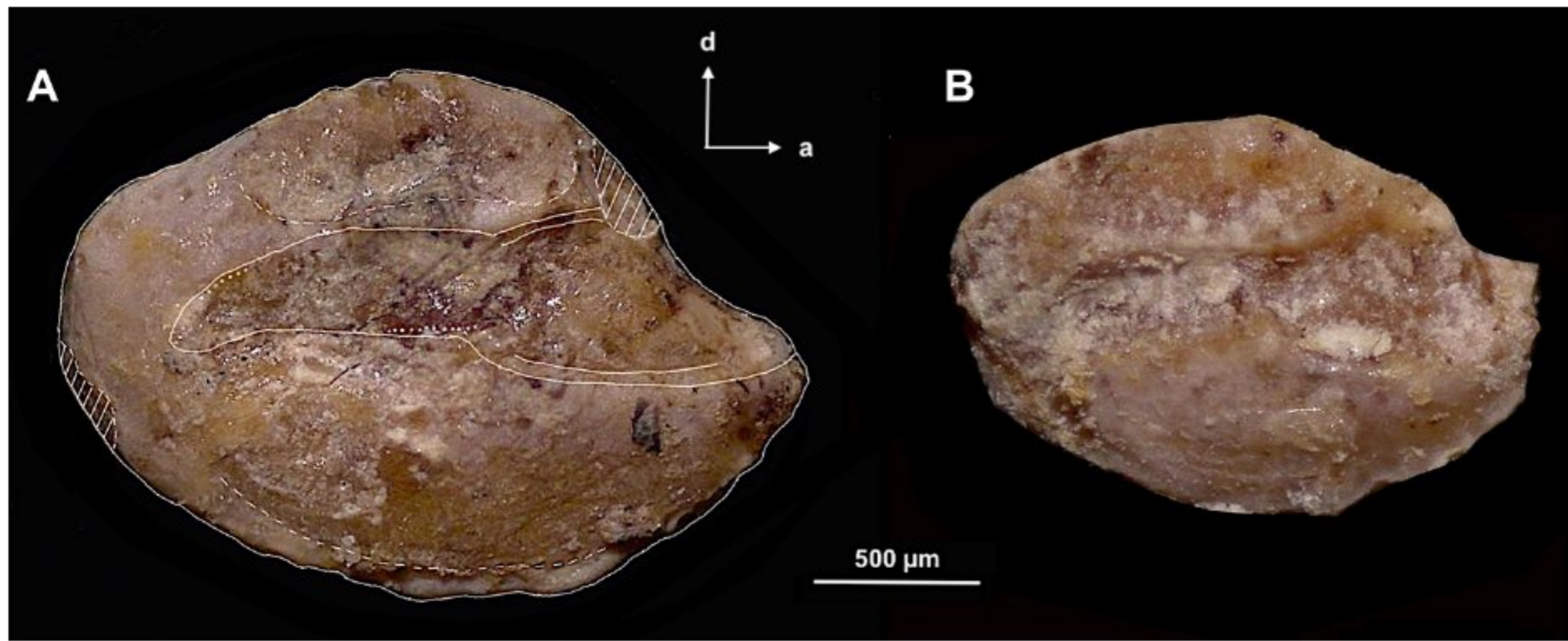Caudal fins are missing in both specimens.

Figure 5. – *Dapalis pauciserratus* n. sp. Otolith A: GZS-RA1, from holotype, interpretative outline of inner face; hatched = damages (chipped). Otolith B: GZS-RA5, from paratype.

Table IV. – Comparison of (i) ostium length vs. cauda length and (ii) the distance of the terminal end of the cauda to the posterior rim of the otolith in 16 species of *Dapalis* (in alphabetic order). The information was taken from the figures (photos or drawings) of the cited literature. Characters similar to those of *D. pauciserratus* are shaded in grey. One asterisk = the otolith of *D. macrurus* is only known from a superficial drawing; two asterisks = so far, no otoliths are known from *D. minutus*.

	Ostium length vs. cauda length	Cauda distance to posterior rim	Authors
D. angustus	different	distant	Reichenbacher & Weidmann (1992) Reichenbacher & Codrea (1999)
D. borkensis	different	close	Reichenbacher (1995)
D. carinatus	different	close	Reichenbacher & Weidmann (1992)
D. crassirostris	different	close	Weiler (1966) Martini (1983) Reichenbacher (1988, 1993)
D. curvirostris	similar	close	Weiler (1966) Martini (1983) Reichenbacher (1988, 1993)
D. formosus	different	close	Martini (1983) Reichenbacher (1993)
D. hungaricus	different	close	Nolf & Reichenbacher (1999)
D. kaelini	different	close	Reichenbacher (1993)
D. macrurus	*	*	–
D. minutus	**	**	–
D. pauciserratus n. sp.	similar	distant	present study
D. praecursor	different	distant	Gaudant (2007)
D. rhenanus	different	close	Reichenbacher & Cappetta (1999)
D. rhomboidalis	different	close	Reichenbacher & Weidmann (1992)
D. transylvanicus	different	close	Reichenbacher & Codrea (1999)
D. ventricosus	different	close	Nolf & Reichenbacher (1999)

Otolith (Sagitta)

The description is based on the otolith of the holotype and only partially also of the paratype as this otolith is broken anteriorly (Fig. 5).

The otolith is 2.3 mm long and 1.6 mm high in the holotype (GZS-RA1), the ratio of otolith length to height is 1.4. The otolith is 1.2 mm high in the paratype (GZS-RA5), its anterior end is broken. The otolith has an oval shape and is moderately elongated. Anteriorly it is moderately pointed and posteriorly rounded. The rostrum is massive with a mod-

erately pointed tip and asymmetrical with concave dorsal and convex ventral margins (rostrum damaged in the paratype). The antirostrum is short, indistinct (damaged in the holotype) and the excisura is shallow and indistinct. Inner and outer faces of the otoliths of the holotype and of the paratype are convex, with the outer face somewhat more prominently. The dorsal rim is gently curved, highest at its middle and rounded in the holotype, somewhat shallower in the paratype. There are no distinct angles along the dorsal rim. The ventral rim is broadly and regularly curved and slightly

undulating. The ventral furrow runs close to and along the ventral rim. This furrow separates the shallow and narrow ventral rim from the dome-shaped ventral area of the inner face. The posterior rim is rounded. There is no postcaudal depression.

The sulcus is well-defined and its overall shape is characteristic for *Dapalis*. The cauda is relatively short and only very slightly bent. The ostium is large, elongate; its lower rim is slightly expanded, nearly straight along most of its course and its upper rim slightly less strongly expanded. The cauda is almost straight, terminally slightly bent and closed, less deep than the ostium and terminates far from the posterior rim of the otolith (Table IV). Cauda and ostium are of about equal length (Table IV). The ratio otolith length to sulcus length is 1.2, the ratio ostium length to cauda length is 0.88. The crista superior and crista inferior are well expressed. Dorsal to the sulcus extends the dorsal depression, which is moderately deep and oval in shape.

DISCUSSION

Skeletons

Dapalis pauciserratus n. sp. is known from two articulated skeletons from Raljin (Serbia). This species differs from all congeners with documented skeletons by its nearly complete absence of serration on the head and of the opercular bones. Generally, the serrations of the opercular series and the infra- and supraorbital bones are of taxonomic importance and often species- specific in this group (Fraser-Brunner, 1954; Martin and Heemstra, 1988; Allen and Burgess, 1990; Schultz, 2000). Ambassid fishes have a maximum of seven serrated ridges or margins on head structures, *e.g.*, the preopercle, interopercle, suborbitals (infraorbitals) and supraorbitals (Fraser-Brunner, 1954). Especially the infra- and supraorbitals are delicate bones, which hardly or only incompletely fossilize. In contrast, the preopercle of *Dapalis* is a robust bone and often well preserved in fossils. Therefore, its shape and serration are important morphological tools for defining the species of this genus (*e.g.*, Weiler, 1955; Gaudant, 1992; Schultz, 2000).

Generally, the posterior and ventral margins of the preopercle of *Dapalis* are completely serrated, with serrations increasing in length from dorsal to ventral (Agassiz, 1833-1843; Schultz, 2000) and relatively long, spine-like serrations are positioned around the bent where both preopercular limbs meet as well as along the ventral margin of the horizontal limb of the preopercle (*e.g.*, Gaudant, 1992; Schultz; 2000). These serrations are slender, pointed and have narrow bases in species with documented preopercles like *Dapalis formosus*, *D. macrurus*, and *D. minutus* (Schultz, 2000) and *D. praecursor* Gaudant, 2007 (Gaudant, 2007) (Figs 6-7).

Dapalis pauciserratus n. sp. on the other hand, has only two large serrations at the angle of the two preopercular limbs. They have the shape of an equilateral triangle and their bases are broad. There are indications of a third spine on the extension of the ventral edge of the preopercle.

Furthermore, *Dapalis pauciserratus* n. sp. differs from *D. minutus* in a (i) shorter predorsal length (41.2% of SL vs. 48.7% of SL), (ii) more slender body (24.2% of SL vs. 35.9% of SL) and narrower head (77.7% of head length vs. 90.2% of head length), (iii) long first spine of the first dorsal fin (42.6% of length of the second spine vs. 18.6% of length of the second spine), (iv) long first spine of the anal fin (69.8% of the length of the second spine vs. 26.3% of the second spine) and (v) short second spine of anal fin (12.1% of SL vs. 22.0% of SL).

In addition, *Dapalis pauciserratus* n. sp. differs from *D. macrurus* in a (i) short predorsal length (41.2% of SL vs. 43.4% of SL) (ii) slender body (24.2% of SL vs. 29.3% of SL) and narrower head (77.7% of head length vs. 86.0% of head length), (iii) short snout (22.7% of head length vs. 29.2% of head length), (iv) large eye (36.2% of head length vs. 29.6% of head length), long first spine of the first dorsal fin (42.6% of length of the second spine vs. 27.2% of
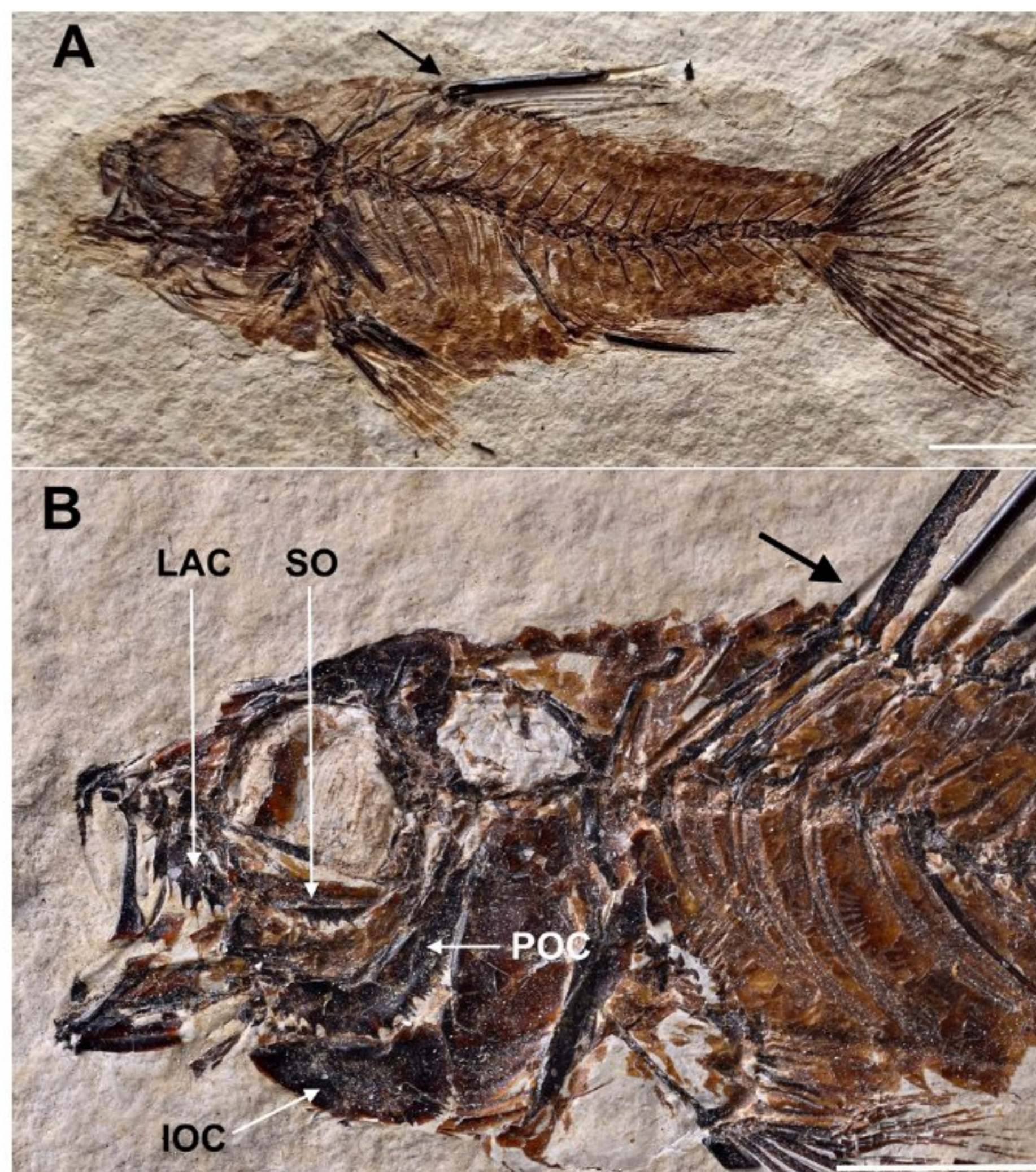

Figure 6. – *Dapalis minutus*, Aix-en-Provence, Late Oligocene. **A**: NHMW 2400; note compact body shape and long, strong second spines of the first dorsal fin and of the anal fin. **B**: MNHN Aix 243; note continuous serration of the preopercle and of the suborbital (infraorbital). LAC, lacrimal (first infraorbital, preorbital); IOC, interopercle; POC, preopercle. Black arrows point to the very short first spine of the first dorsal fin. Scale bars are 10 mm.
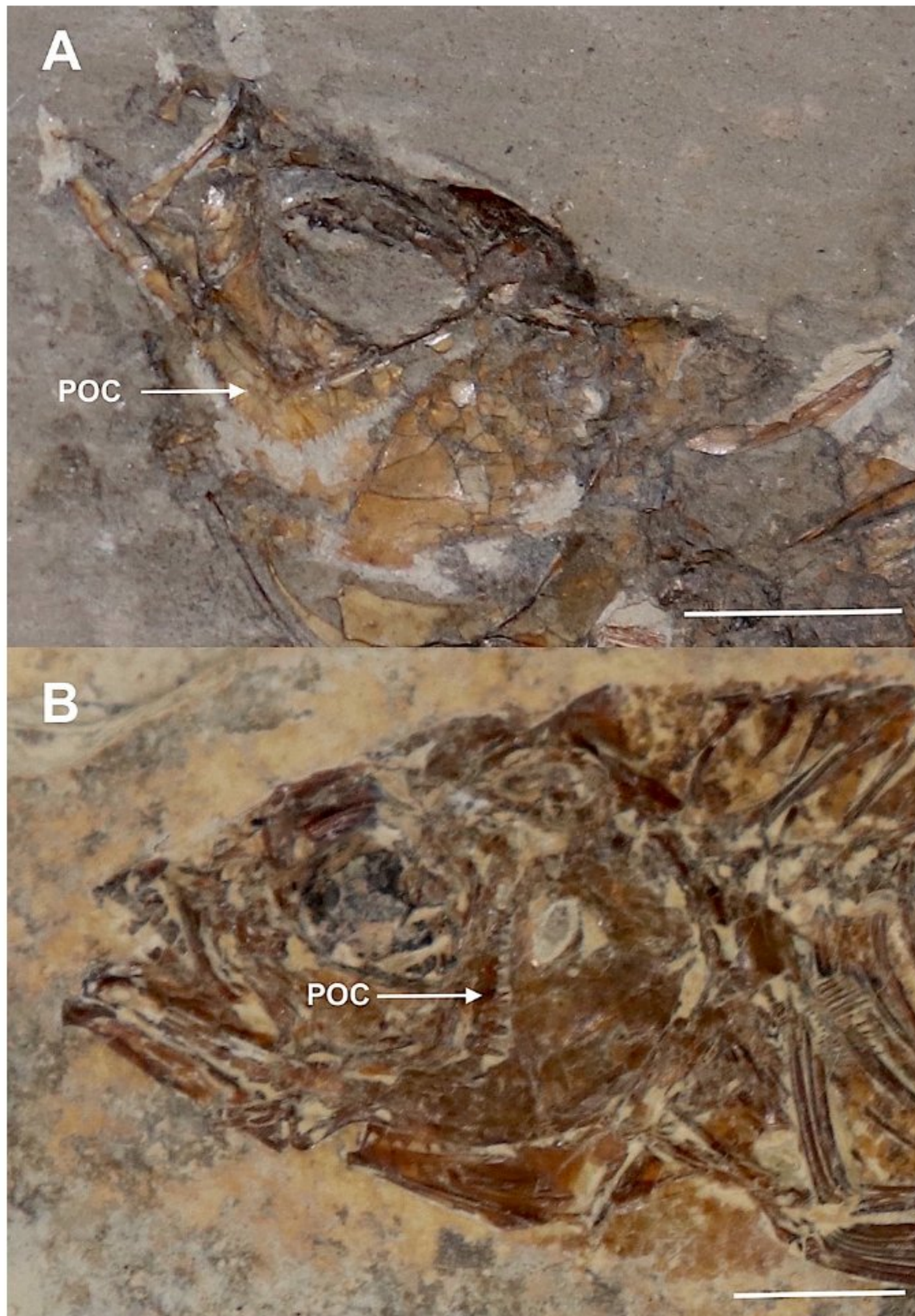
Figure 7. – Serrated preopercle (POC) with many spines of (**A**) *Dapalis formosus* (SMNS 002960) from Unterkirchberg (Germany) and (**B**) *Dapalis macrurus* (SMNS 55544) from Céreste (France). Scale bars are 5 mm.

Figure 8. – Compartmentalized internal structure of the dorsal-fin spines of (**A**) *Dapalis pauciserratus* n. sp., holotype (GZS-RA1) and (**B**) a cleared and stained specimen of the extant *Parambassis bacculis* (UF 178036). The black and white arrow points to the internal structure of the dorsal spines, visible in *Dapalis pauciserratus* n. sp. (holotype) just where the surface of the third spine is chipped. a = anterior, d = dorsal. Scale bars are 2 mm.

length of the second spine), (v) long first spine of the anal fin (69.8% of the length of the second spine vs. 30.4% of the second spine) and (vi) short second spine of anal fin (12.1% of SL vs. 15.4% of SL).

Seemingly, the length of the first two spines of the dorsal fin and of the anal fin are a character which allows differentiation of at least some of the species known by skeletons. Especially *Dapalis minutus* has a very short first and a long second spine in these fins, whereas the first spine is distinctly long in *D. pauciserratus* n. sp. and intermediate in *D. macrurus* (but closer to the status of *Dapalis minutus* (Figs 3, 6; Table II). Seemingly characteristic for Ambassidae is the compartmentalized internal structure of the fin spines (Roberts and Jumnongthai, 1999) (Fig. 8). In the holotype the surface of the third spine of the first dorsal fin is chipped and the compartmentalized internal structure is visible (Fig. 8). Most extant freshwater ambassids from Asia have such internal structure (Roberts and Jumnongthai, 1999), but no specific names were mentioned by these authors. We found such
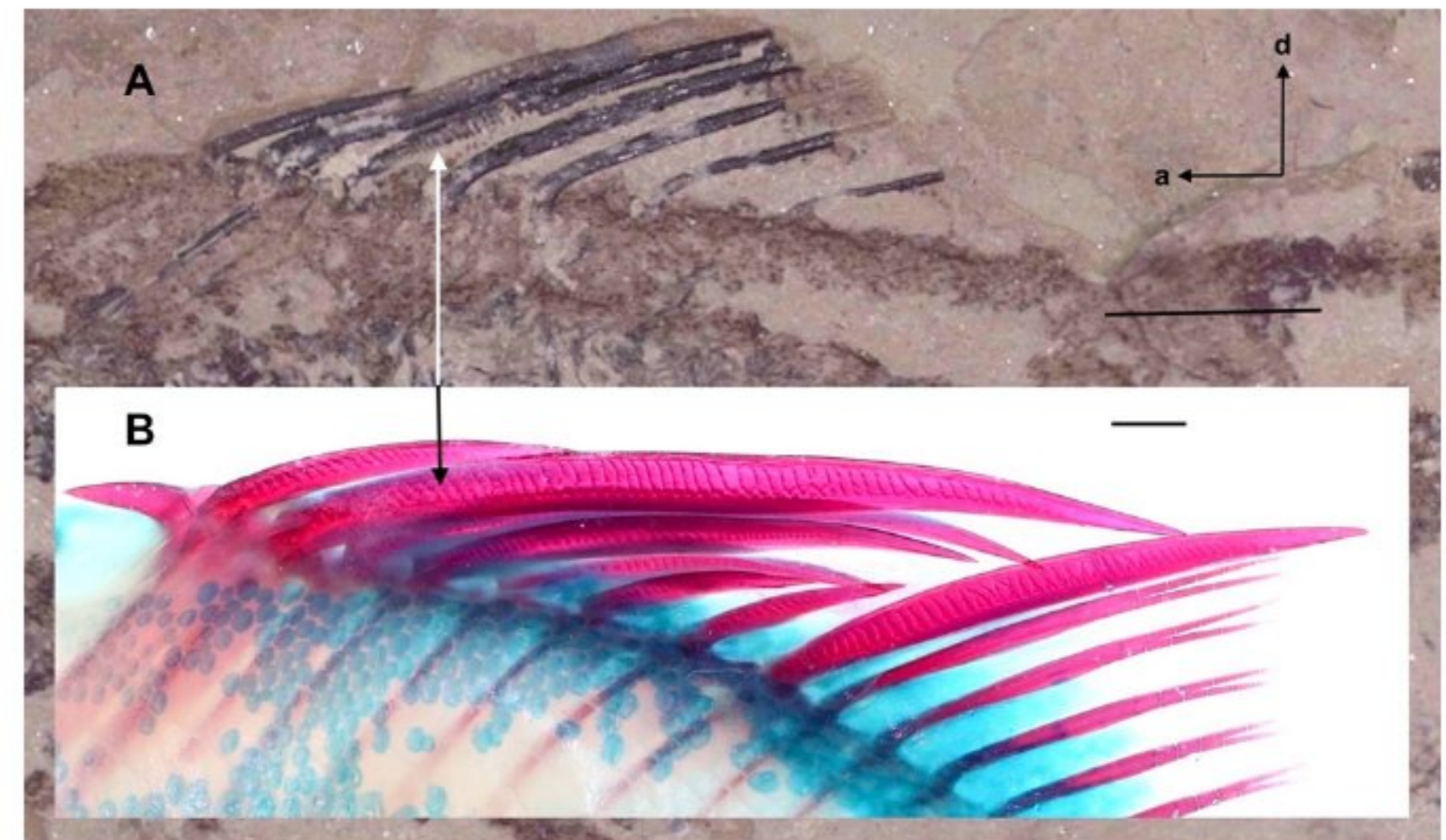
internal structures in the following ten brackish- and freshwater inhabiting ambassid species from ~~five~~ four genera: *Ambassis agrammus* Günther, 1867, *Ambassis buruensis* Bleeker, 1856, *Ambassis dussumieri* Cuvier, 1828, *Ambassis macleayi* (Castelnau, 1878), *Denariusa australis* (Steindachner, 1867), *Gymnochanda ploegi* Tan & Lim, 2014, *Parambassis baculis* (Hamilton, 1822) (Fig. 8), *Parambassis lala* (Hamilton, 1822), *Parambassis siamensis* (Fowler, 1937) and *Parambassis piratica* Roberts, 1989. Information on the spine structure from other members of the family and from other acanthomorph fishes is needed for comparison and to verify if these internal structures of the spines could be a synapomorphy of the Ambassidae.

Otoliths

As stated above, only rather few *Dapalis* species are based on osteological remains (*e.g.*, *D. formosus*, *D. macrurus*, *D. minutus*) (*e.g.*, Agassiz, 1833-1843; Meyer, 1852; Weiler, 1955; Gaudant, 1978, 1992; Gaudant *et al.*, 2018). The majority of fossil species of *Dapalis* are established based on otoliths alone (*e.g.*, Brzobohatý and Schultz, 1973; Reichenbacher, 1988, 1993; Reichenbacher and Weidmann, 1992; Nolf and Reichenbacher, 1999; Reichenbacher and Codrea, 1999; Uhlig *et al.*, 2000). Most of the species of *Dapalis* from Oligocene deposits of Europe are documented from lacustrine freshwater to brackish sediments. So far, four otolith-based species are known from the early Lower Oligocene, *D. angustus*, *D. borkensis* and *D. transylvanicus* and *D. macrurus*, the latter being as the only one known from otoliths *in situ* (see Table I for references). One species with otoliths in situ, *D. praecursor*, has been described from the Middle Eocene (Gaudant, 2007). *Dapalis transylvanicus* is possibly the ancestor of *D. carinatus* and *D. rhomboidalis* of the Late Oligocene (Reichenbacher and Codrea, 1999).

Dapalis pauciserratus n. sp. differs from *D. praecursor* in (i) a more roundish shape vs. a more elongate shape (the range of otolith hight to otolith length, is 1.3 vs. 1.55), (ii) a massive rostrum with a rounded moderately pointed tip vs. a moderately sized rostrum with a pointed tip, (iii) ostium and cauda of about the same length vs. ostium shorter than cauda and, (iivi) terminal end of cauda slightly bent and closed vs. cauda straight and terminal end open.

Dapalis pauciserratus n. sp. differs from *D. angustus* in (i) the wider and longer ostium, which is also more strongly expanded ventrally, (ii) the inner and outer surface of the otolith are convex vs. inner and outer surface of the otolith are flat, (iii) the wider and longer ostium, which is also more strongly expanded ventrally and, (iv) the distinct, asymmetric rostrum with concave dorsal and convex ventral margin vs. rostrum prominent, symmetric with dorsal and ventral margin straight or convex.

Dapalis pauciserratus n. sp. differs from *D. transylvanicus* in (i) outer face of otolith slightly convex vs. outer face strongly convex, (ii) no posterodorsal angle vs. posterodorsally expanded, (iii) ostium narrow, long vs. ostium wide, short (ostium length to cauda length = 1.05 vs. 0.85-0.9) (iv) cauda terminating far from posterior rim of otolith (otolith length to sulcus length = 1.2) vs. cauda terminating close to posterior rim of otolith (otolith length to sulcus length = 1.1-1.15) (Table IV).

Dapalis pauciserratus n. sp. differs from *D. borkensis* in (i) dorsal rim gently curved, rounded vs. dorsal rim with sharp middorsal angle, (ii) ostium narrow, long vs. ostium wide, short (ostium length to cauda length = 1.05 vs. 0.75) and (iii) cauda straight, terminally slightly flexed vs. cauda straight.

Dapalis pauciserratus n. sp. differs from *D. macrurus* found *in situ* (Weiler, 1939, refigured in Martini, 1965) in (i) in the more elongate shape (otolith length to height = 1.3 vs. approximately 1.2). The drawing of Weiler is very schematic depicting an otolith of a presumably juvenile fish without diagnostic features.

Dapalis pauciserratus n. sp. differs from *D. carinatus* in (i) the absence of a posterodorsal angle vs. posterodorsal angle present, (ii) cauda terminating slightly flexed and ending distant from posterior rim vs. cauda straight and reaching close to the posterior rim (Table IV).

Dapalis pauciserratus n. sp. differs from *D. rhomboidalis* in (i) oval shape vs. roundish shape, (ii) ostium about as long as cauda vs. ostium distinctly shorter than cauda (ostium length to cauda length 1.05 vs. 0.75), (iii) cauda terminating distant from posterior rim vs. cauda terminating near posterior rim (Table IV).

In conclusion it must be mentioned that the otoliths of *Dapalis* mostly show few diagnostically useful features and that many of the nominal otolith-based species are rather similar morphologically. However, in the case of *Dapalis*

pauciserratus n. sp. the combination of two characters, (i) the ostium being about as long as the cauda or slightly longer and (ii) the termination of the cauda far from the posterior rim of the otolith, seem to be features reliably separating the species from most known fossil otolith-based species of the genus (Table IV) and hence support the recognition of a new species as described based on skeletal features. Nevertheless, in *D. angustus*, *D. curvirostris* and *D. praecursor* one of these two characters is similar to those of *D. pauciserratus*, character (i) in the Miocene *D. curvirostris* and character (ii) in the Oligocene *D. angustus* and in the Eocene *Dapalis praecursor* (Table IV).

Our results support observations made with gobioid fishes from the Lower Miocene sediments (Bradić-Milinović *et al.*, 2019) and indicate the level of diversity of fishes that was present in the freshwater habitats of the Oligocene-Early Miocene systems of southeastern Europe.

Paleobiogeographic considerations

The family Ambassidae today is restricted to environments along the shores of the Indo West-Pacific and the freshwater habitats on the adjacent continents. Fossils have been found primarily in Europe from late Eocene to Middle Miocene (Gaudant, 1978, 1992; Reichenbacher, 1988, 1993, 1995, 1998, 1999), but a few records of otolith-based ambassids exist as well from the early to late Eocene of New Zealand (Schwarzhans, 2019). The European records are from freshwater and brackish water environments and are all placed in the fossil genus *Dapalis* (see above). The New Zealand records stem from shallow marine sediments and are thought to represent the genus *Ambassis* sensu lato. Fossil records of ambassid otoliths from the Maastrichtian of India (*Dapalis erici* Nolf *et al.*, 2008 and *Ambassis*? *cappettai* Rana & Sahni, 1989) are small, plesiomorphic acanthomorph otoliths that may or may not represent basal Perciformes but require review and should not be taken for Ambassidae at the current status.

The family Ambassidae has recently been analysed for molecular phylogeny (Verma *et al.*, 2019; Ghazali *et al.*, 2019, 2023) with in part rather divergent results. Some of the studies imply systematic consequences. The origination of Ambassidae is concluded as of early Paleogene age, Paleocene to early Eocene, in all three studies. This interpretation is in line with the fossil record but none of the studies actually included paleontological data into their analysis. Ghazali *et al.* (2019, 2023) assumed the Ambassidae to be of Indo West-Pacific origin, which is consistent with the earliest finds in New Zealand. These studies also reflected on the origin of the Ambassidae as marine fishes (Ghazali *et al.*, 2019) versus a freshwater origin (Ghazali *et al.*, 2023). From the paleontological evidence at hand, a marine origin appears more likely. However, a marine origin would require multiple evolutionary migration paths into freshwater, including

the one represented by the fossil genus *Dapalis* in Europe that became extinct during the Miocene. We would like to plead at this occasion for future phylogenetic and phylogeographic assessments to make use of the fossil data base available in order to arrive at a full evidence analysis.

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