Skeletal remains with otoliths *in situ* of the Miocene croaker *Trewasciaena* cf. *kokeni* (Teleostei, Sciaenidae) from the Pannonian of the Vienna Basin

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Two articulated skeletons of juvenile sciaenids referred to *Trewasciaena* cf. *kokeni* based on their saccular otoliths preserved *in situ* are described herein. The specimens provide the only available skeletal evidence of the genus *Trewasciaena* in the record and are characterized by moderately cavernous frontals, poorly developed supraoccipital crest, premaxilla bearing a large articular process with rounded dorsal margin, dentary and anguloarticular firmly articulated, lower jaw joint located in level of anterior half of orbit, jaw teeth small and probably arranged in single row, preopercle crescent shaped with small and regularly spaced spines along the posterior border of its vertical arm, vertebral column apparently containing 24 vertebrae, seven pairs of ribs, caudal skeleton with five autogenous hypurals, slender parhypural, two uroneurals and three epurals, haemal spines of the second and third preural vertebrae autogenous, neural spine of second preural vertebra reduced, elongated dorsal fin with ten or eleven spines and 23 soft rays, short-based anal fin with two spines and probably four soft rays, second anal spine much longer than the first one, pectoral fin probably composed of eight short rays, body densely covered by scales. Despite the potential relevance of these specimens for our understanding of the relationships of *Trewasciaena* within the Sciaenidae, the concurrent effect of their incompleteness, inadequate preservation and juvenile nature prevented any conclusive statement about the phylogenetic position of this extinct genus, which remains elusive. • Key words: Sciaenidae, Pannonian, Miocene, articulated skeleton, otoliths *in situ*, Vienna Basin.

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The Sciaenidae is a speciose family of percomorph fishes that comprises more than 280 extant species arranged in 67 genera, which inhabit marine, brackish and freshwater environments worldwide (Nelson *et al*. 2016). These fishes are known for their ability to vocalize, for which they are commonly named drums or croakers (see, *e.g.* Sasaki 1989, Ramcharitar *et al*. 2006). The fossil record of this group is primarily represented by the otoliths that are especially common and abundant in Neogene clastic deposits (see, *e.g.* Schwarzhans 1993, Nolf 2013). Sciaenid otoliths are taxonomically informative because of their large size and species-specific morphology, being commonly used also to separate the extant members of the family. Conversely, fossil articulated skeletal remains are relatively rare (see Bannikov *et al.* 2009, 2018; Bannikov 2010; Otero *et al.* 2013) and their systematic interpretation is complicated by the fact that the classification of the extant members of this family is primarily based on soft anatomical features, including pores on snout and lower jaw, barbels, lateral-line morphology, cavernous canals on the head, and morphology of the swimbladder (see Trewavas 1962, 1964, 1977; Chao 1978, 1986, 2002, 2016; Sasaki 1989; Walker & Radford 1992; Nelson *et al*. 2016). In this context, an unique opportunity to properly interpret the affinities of fossil sciaenids is represented by skeletal remains with otoliths preserved *in situ* (see, *e.g.* Schwarzhans & Carnevale 2017, Schwarzhans *et al*. 2018), as recently demonstrated by Bannikov *et al*. (2018) based on Paratethyan material.

Here we describe two sciaenid articulated skeletons with otoliths *in situ* from the Pannonian of the Vienna Basin. The otoliths *in situ* suggest that the fossils pertain to the extinct genus *Trewasciaena*, thereby providing the first known record of skeletal remains of this genus.

Figure 1. Sketch map of the Vienna Basin showing the position of the Ratíškovice village. Modified from Kováč *et al*. (2008).

The main goal of this paper is therefore to provide a descriptive analysis of these fossils and discuss their possible affinities within the Sciaenidae.

Geological note

The fossils described herein were collected from the organic rich laminated argillites overlying the Dubňany Seam (Dubňany or Ratíškovice; Fig. 1) in one of the Dubňany lignite mines located in the South Moravian lignite district, Vienna Basin.

The Dubňany lignite seam developed within Pannonian sediments representing the younger of the two main lignitiferous layers in the area (Čtyroký 2000, Honěk *et al*. 2010). It is lying at the base of the lowermost "cyclotheme" ("F1" level; Jiříček 1985) of the Dubňany Formation (Čtyroký 2000). Although we are unable to definitely confirm the origin of the fossils described herein (see below), Honěk *et al*. (2010) mentioned the presence of abundant fish remains in the argillites of the second overlying level of impermeable rock developed within Dubňany Fm. ("Zone F", according to Papp 1951). These deposits originated along the northern margins of the Vienna Basin in a sedimentary context dominated by argillites and clays alternated with sandy layers (Honěk *et al*. 2010).

The general regressive trend and the regional transition to brackish and/or freshwater environments during the Pannonian (Harzhauser *et al*. 2004, Honěk *et al*. 2010) suggest that brackish or freshwaters occurred in the original palaeobiotope. The analysis of pollens and dinoflagellates from the "Zone F" are indicative of floodplain and swampy vegetation (with occasional higher salinity) within an open and possibly weakly vegetated landscape (Doláková & Kováčová 2008, Honěk *et al.* 2010).

Material and methods

According to original documents associated with the argillitic slabs, it seems that they were collected in 1958 in the "Mine C" (= former name of the Mine Osvobození) within the "overburden of Dubňany seam". On the other hand, the information written directly on the slab of rock indicates the locality "GV1" and depth 106 m. According to Knobloch (1969), fossil material from "Dubňany" may derive from three different sites, mines "1. máj", "Osvobození" and ventilation shaft "GV1", although the material from the first two sites was collected in the mine dumps.

The argillitic slabs that include two fish specimens with otoliths preserved *in situ* (as a part and counterpart; Fig. 2) are housed in the Paleontological Department of the National Museum in Prague with the numbers NMP Pv11673 and NMP Pv11674. The sagitta removed from one of the fossils was recognized as belonging to a juvenile individual referred to as *Trewasciaena* cf. *kokeni* (Schubert, 1902) by R.B. and used as a primary taxonomic indicator.

The specimens were examined using a Leica Stereomicroscope Leica MZ6 equipped with a camera lucida drawing arm. The photos were prepared using a Canon EOS 1000D associated with the stereomicroscope.

Anatomical abbreviations: aa – anguloarticular; br – branchiostegal rays; bsph – basisphenoid; CaL – cauda lenght; cv – caudal vertebra; d – dentary; epu – epural; fr – frontal; hm – hyomandibula; hspu – haemal spine of the preural vertebra; hyp – hypural; mx – maxilla; OH – otolith height; OL – otolith length; op – opercle; OsH – ostium height; OsL – ostium length; pg – pterygiophore; php – parhypural; pmx – premaxilla; pop – preopercle; psph – parasphenoid; ptsph – pterosphenoid; pu – preural vertebra; q – quadrate; ra – retroarticular; ry – fin ray; sg – sagitta; SL – standard length; soc – supraoccipital; sp – fin spine; sy – symplectic; TL – total length; un – uroneural.

Systematic part

Family Sciaenidae Cuvier, 1829

Genus *Trewasciaena* Schwarzhans, 1993

***Trewasciaena* cf. *kokeni* (Schubert, 1902)**
Figures 2–7

? 1902 *Otolithus* (*Sciaenidarum*) *Kokeni*; Schubert, pl. 10, fig. 18.
? 2013 *Trewasciaena kokeni* (Schubert, 1902). – Schultz, p. 328, pl. 91, figs 1–5. (cum syn., *non* fig. 3a, b).
? 2018 *Trewasciaena kokeni* (Schubert, 1902). – Bannikov *et al*., fig. 8f–j.

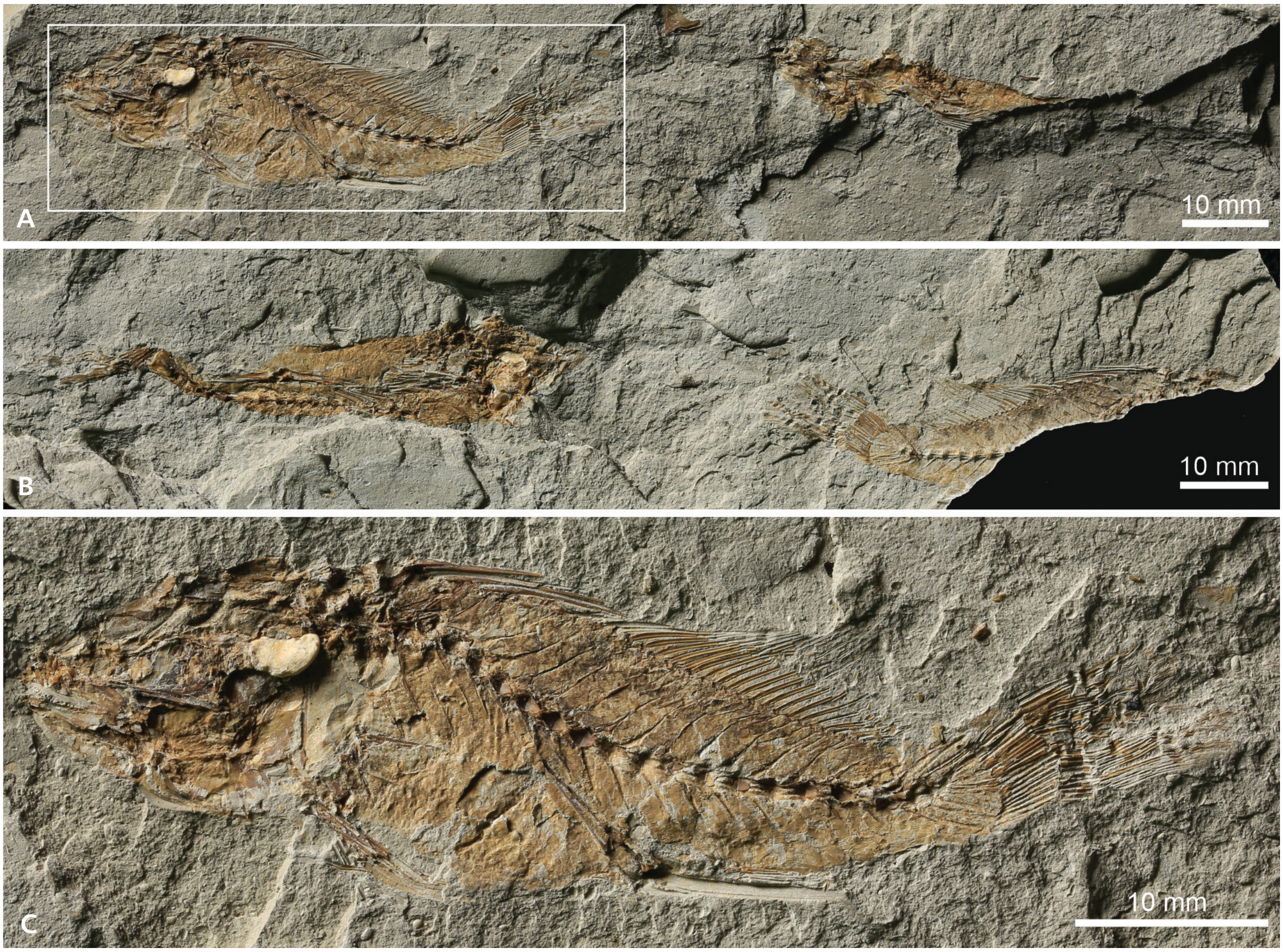

Figure 2. Articulated skeletons of *Trewasciaena* cf. *kokeni* (Schubert, 1902) with otoliths *in situ*; A – slab including NMP Pv11674a (left) and NMP Pv11673b (right); B – counterpart of the slab in A, including NMP Pv11673a (left) and NMP Pv11674b (right); C – NMP Pv11674a, left lateral view.

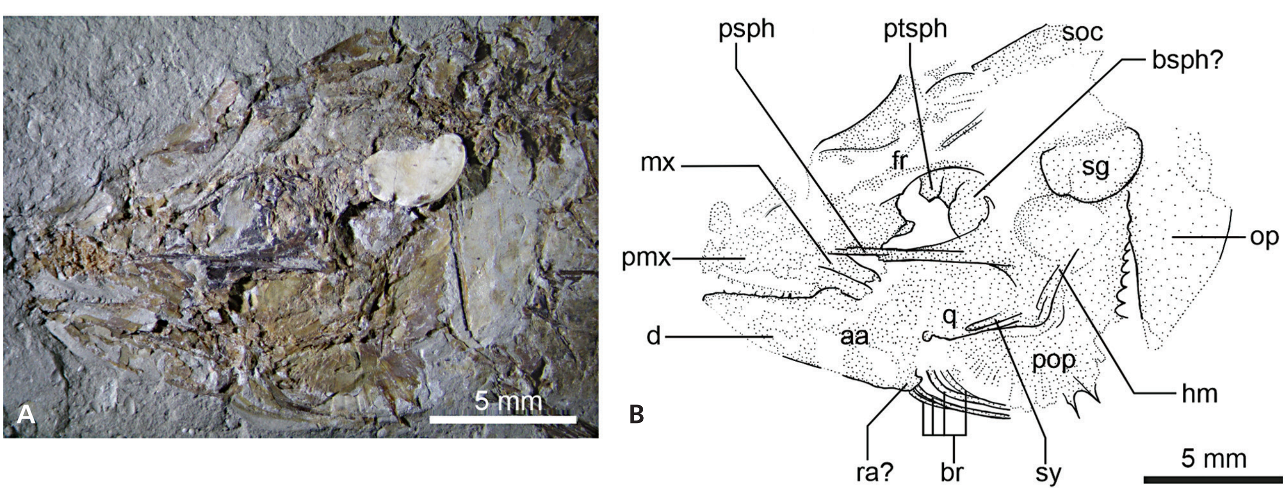

Figure 3. *Trewasciaena* cf. *kokeni* (Schubert, 1902); A – head of NMP Pv11674a, left lateral view; B – interpretative drawing.

For full synonymy and cited occurrences of the *T. kokeni* see Schultz (2013). Other synonyms are: *Otolithus* (*Sciaenidarum*) cfr. *loczyi* – Lörenthey (1906, pl. 3, fig. 24, *non* fig. 23), *Umbrina* sp. – Carnevale *et al*. (2006, fig. 3b), *Trewasciaena kokeni* (Schubert, 1902) – Bannikov *et al*. (2018, fig. 8f–j). Some other tentative synonymy data are: *Trewasciaena kokeni* (Schubert, 1902) – Bosnakoff (2008, pl. 3, figs 1–8); "genus aff. *Umbrina*" *kokeni* (Schubert, 1902) – Bosnakoff (2011, fig. 5o);

Figure 4. *Trewasciaena* cf. *kokeni* (Schubert, 1902). Left sagitta of NMP Pv11673c; A – interpretative drawing (inner face); B – inner face; C – outer face.

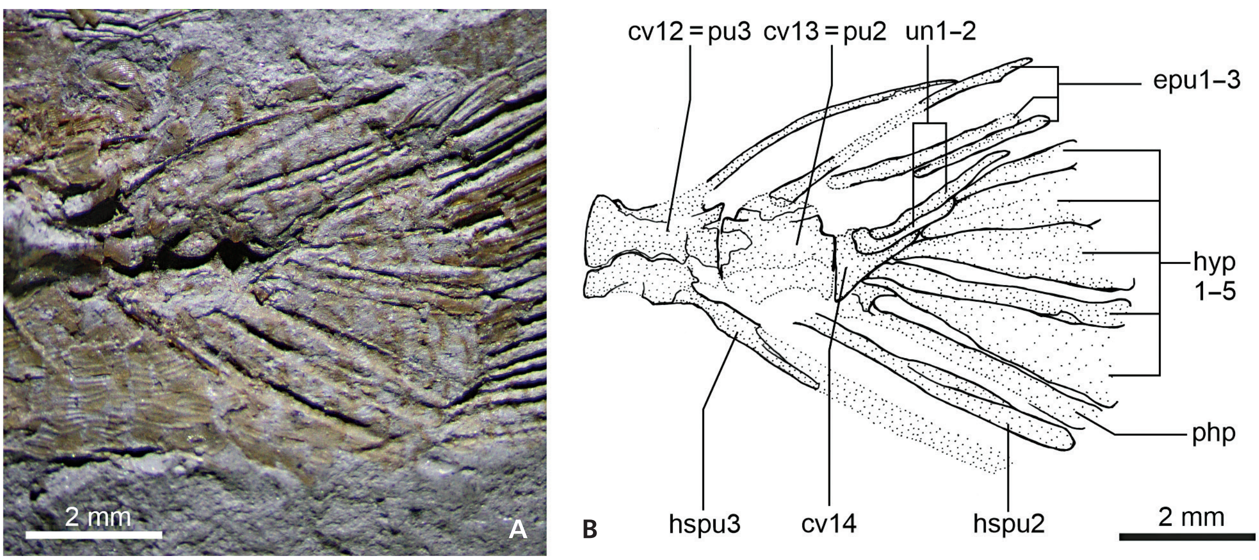

Figure 5. *Trewasciaena* cf. *kokeni* (Schubert, 1902); A – caudal skeleton of NMP Pv11674a; B – interpretative drawing.

"*Trewasciaena*" sp. – Colombero *et al*. (2017, fig. 5.14), and "*Trewasciaena*" sp. – Carnevale *et al*. (2018, fig. 3r).

Material. – NMP Pv11673, a partially complete and poorly preserved articulated skeleton with otolith *in situ*. Specimen NMP Pv11674, a partially complete, moderately preserved, articulated skeleton with otolith *in situ*, in part and counterpart; SL = 50.9 mm, TL = 63.8 mm.

Description. – Measurements (in % of SL; based on NMP Pv11674): head length = 35.6; head depth = 25.9; caudal fin length = 25.3; caudal peduncle length = 8.5; predorsal length = 37.5; preanal length = 60.1; prepelvic length = 31.63; dorsal-fin base length = 51.1; anal-fin base length = 11.4; length of first anal-fin spine = 5.1.

Otolith measurements (in mm; Fig. 4): otolith length (OL) = 3.9; otolith height (OH) = 2.4; OL/OH = 1.6; CaL/OsL = 1.1; OsL/OsH = 1.34.

The body is moderately elongate and the head is almost triangular in lateral view. The dorsal profile of the body is convex while the ventral profile is almost straight.

The head (Fig. 3) is poorly preserved in both available specimens, with bones extensively crushed and difficult to distinguish from each other. The frontals appear to be moderately cavernous dorsally and bear a ventral interorbital laminar extension. The supraoccipital crest is poorly developed. In the posterior wall of the orbit the pterosphenoid and what appears to be the basisphenoid are recognizable in NMP Pv11674. The parasphenoid is stout, and almost straight.

The mouth is terminal, with a gape extending posteriorly up to the anterior margin of the orbit. The premaxilla seems to possess a large articular process with a rounded dorsal margin. The maxilla is poorly preserved. The mandible is thick with firmly articulated dentary and anguloarticular, which form a moderately developed coronoid process originating at the end of the dentary tooth row. The lower jaw joint is located in the level of the anterior half of the orbit. A tiny quadrangular retroarticular is recognizable at the posteroventral corner of the

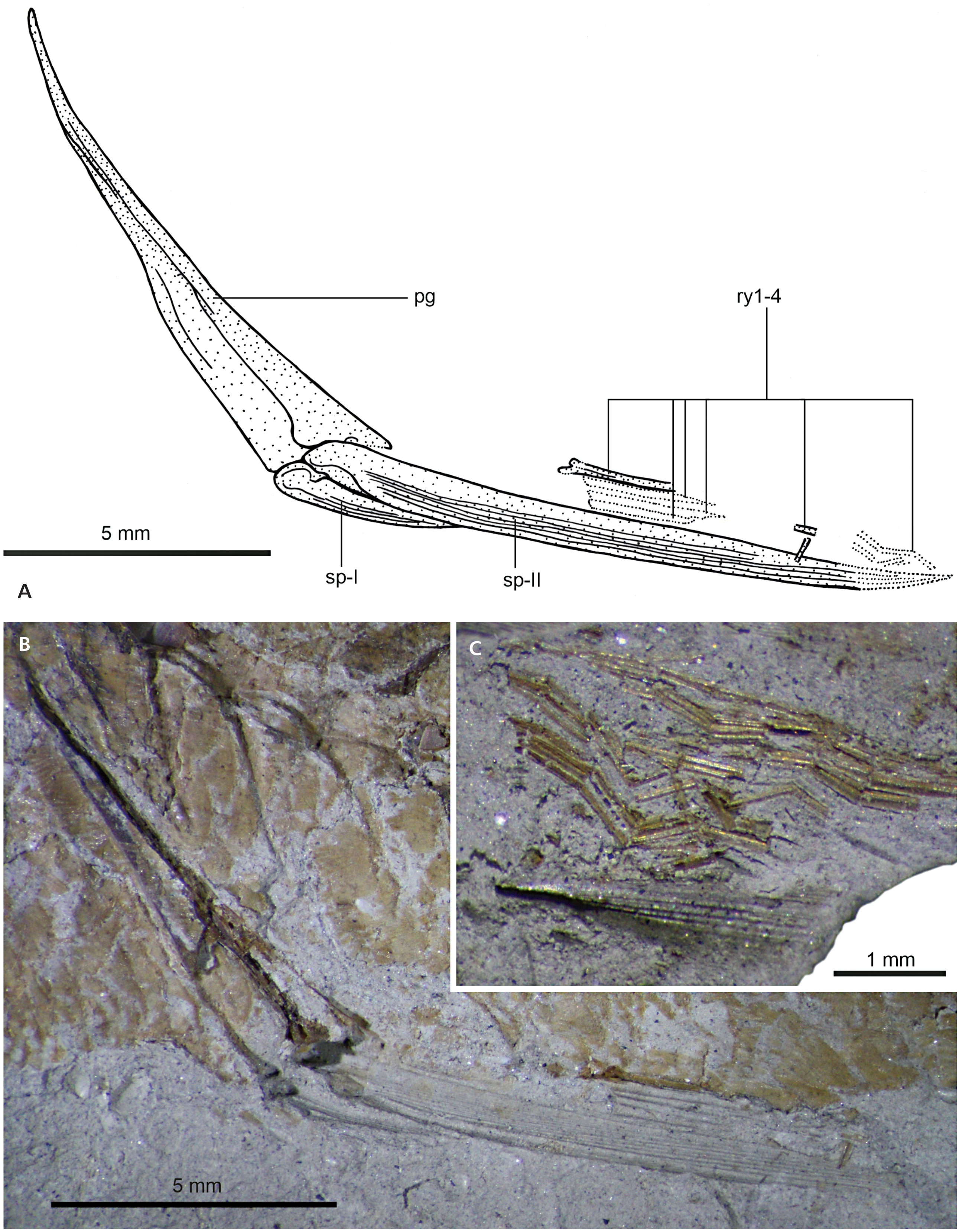

Figure 6. *Trewasciaena* cf. *kokeni* (Schubert, 1902). Anterior part of the anal fin of NMP Pv11674; A – interpretative drawing (based on part and counterpart); B – NMP Pv11674a, left lateral view; C – anal-fin rays of NMP Pv11674b, right lateral view.

mandible. Both the upper and lower jaws bear small teeth probably arranged in a single row. The original number of teeth is difficult to determine. Of the supensorium only part of the quadrate, a posterodorsally expanded symplectic and the opercular process of the hyomandibula are preserved and recognizable in NMP Pv11674. The preopercle is crescent shaped and bears small and regularly spaced spines along the posterior border of its vertical arm; a couple of large spines are also present at the angle formed by the vertical and horizontal arms, although the original complement cannot be properly defined. The opercle is a laminar bone with a linear and vertical anterior margin. A robust hyoid bar is partially preserved together with an indeterminate number of poorly preserved branchiostegal rays.

The saccular otoliths (sagittae) are exposed in the otic region of the neurocranium (Figs 2–3) of both the specimens. The left sagitta has been extracted from the specimen NMP Pv11673. The overall morphology of the sagitta (Fig. 4) is indicative of the juvenile nature of the individuals. The outline is elliptic with concave ventral rim and approximately centrally laying deepest point (OL/OH = 1.58). The dorsal rim is weakly undulated in the middle part. The anterior rim is rounded with a weekly protruding ostial colliculum. The inner face is slightly convex, the outer face mildly concave and without umbo. It shows the typical sciaenid sulcus that is distinctly supramedian. The oval ostium narrows anteriorly and is clearly restricted in the middle and is also characterized by a clearly precaudal depression. The cauda is long, narrow, and deepened, with its rear part bent downward forming an angle of 90° with the horizontal part, ending slightly below the lower level of the ostium. The horizontal section of the cauda is slightly longer than the ostium. A ventral furrow is weekly developed and runs parallel to the ventral rim. A well-developed, relatively high and deep dorsal depression is visible above the connection between the ostium and the cauda and follows almost the entire caudal length becoming gradually narrower. The space between the rear margin of the ostium and downturned portion of the cauda measures about 37% of the sulcus length, a typical feature of the genus *Trewasciaena* (see Bannikov *et al*. 2018).

The vertebral column is sigmoid and consists of approximately 24 vertebrae. Despite the anterior part of the vertebral column is not clearly preserved, the abdominal portion appears to contain around ten vertebrae, while the caudal portion consists of 14 vertebrae. There are seven pairs of ribs, the first of which articulates with what appears to be the third abdominal centrum. The caudal skeleton (Fig. 5) contains five autogenous hypurals, a slender parhypural, two uroneurals and three epurals. The haemal spines of the second and third preural vertebrae seem to be autogenous. The neural spine of the second preural vertebra is reduced to a low and almost rounded crest. Due to the inadequate preservation, it is not possible to determine whether the caudal fin is truncate or rounded. There are 17 (9 + 8) elongate principal caudal-fin rays plus four dorsal and four ventral procurrent rays. The predorsal region is poorly preserved in both available specimens and, for this reason, there is no evidence of the original complement of supraneurals. The dorsal fin is notably elongated and contains ten or eleven spines followed by 23 soft rays. The fin is notched due to the shortening of the penultimate spine. The first dorsal-fin pterygiophore bears two supernumerary spines. The anal fin originates just below the fourth and fifth caudal vertebrae. It is relatively short based (slightly more than 10% of SL) and consists of two longitudinally striated spines followed by at least four soft rays. The second spine is much longer and massive than the first one – the second spine is about four times longer than the first spine and about as long as the first soft ray (see Fig. 6). The first anal-fin pterygiophore is strongly inclined and massive. The paired fins and their girdles are scarcely preserved, although fragments of the pectoral fin suggest that it was composed of at least eight rather short rays. The pelvic fins are partially preserved in the specimen NMP Pv11673; they insert slightly anteriorly to the pectoral fins and consist of a single pointed spine and five rays. The distal extremities of the pelvic-fin rays extend backward to the level of the penultimate abdominal vertebra.

The body is densely covered by scales. The head and the proximal part of the caudal fin are covered by small cycloid scales, while the rest of the body is covered with ctenoid scales. Ctenoid scales show a few rows of short ctenii, and well-developed radii, which are present in numbers of seven to nine. The lateral line is not clearly recognizable.

Discussion

Considered to be closely related to the Haemulidae (Trewavas 1977, Schwarzhans 1993), the family Sciaenidae is currently aligned with the Polynemidae based on the shared possession of a suite of muscular and skeletal features (Johnson 1993, Presti *et al*. 2020). Sciaenids can be easily defined based on a number of features that can be regarded as diagnostic of the family (Trewavas 1977, Chao 1978), including large and complex swimbladder and associated well-developed drumming muscles, enlarged lateral-line canals on the head and pores on the snout and lower jaws and extension of the lateral line to the tip of the caudal fin. However, these features are relatively useless from a palaeontological perspective (see Bannikov *et al*. 2018). Sasaki (1989) recognized several features that are potentially observable in fossil articulated skeletal remains (soft dorsal-fin base elongate, typically much longer than anal-fin base; two anal-fin spines; dorsal- and anal-fin pterygiophores bisegmental; frontals cavernous; palatine expanding ventrally; symplectic dorsally flattened, interdigitating medially with the metapterygoid; metapterygoid and quadrate interdigitating medially; supramaxillae absent; palatine toothless; a single branchiostegal articulating with the posterior ceratohyal), some of which have been also observed in the fossils described herein, thereby supporting their placement within the family Sciaenidae. In particular, as documented above, the two fossil fishes from the Pannonian of the Vienna Basin show frontals cavernous, supramaxilla absent, a long-based soft dorsal fin, and two anal-fin spines. The surprisingly reduced complement of anal-fin rays (only four elements) seems to be unique for these fossils although the posterior incompleteness of the fin cannot be ruled out. The otoliths preserved *in situ* unequivocally confirm the familial placement. The usually large saccular otoliths of the Sciaenidae are remarkably distinctive from a taxonomic point of view, being relatively elongated with index OL/OH > 1(usually longer as higher), characteristic sulcus with shorter, wider and shallower ostium and longer, narrower and posteroventrally bent cauda. Both the sides of the sagitta are usually vaulted, the outer one often higher with irregularly bumps and the postcentral umbo. Sciaenid otoliths show a high degree of morphological diversity, as well as a remarkable ontogenetic allometry (*e.g.* Schwarzhans 1993, Nolf 2013). Ontogenetic series of otoliths have been documented for *Umbrina subcirrhosa* and *Trewasciaena kokeni* (*e.g.* Schwarzhans 1993, Nolf 2013).

Unfortunately, juvenile otoliths of sciaenids are often characterized by a few taxonomically relevant features (*e.g.* Bannikov *et al.* 2018). The sagittae *in situ* described herein clearly pertain to juvenile or subadult individuals.

As discussed above, the family Sciaenidae consists of 67 extant genera (Nelson *et al.* 2016), plus a number of extinct genera, including some solely based on otoliths (see Schwarzhans 1993, Bannikov *et al*. 2018). The otoliths preserved *in situ* allowed us to define the generic and specific placement of the examined specimens, which are therefore referred to *Trewasciaena* cf. *kokeni*. This species has been assigned to a variety of genera, including *Otolithus* (*Sciaenidarum*), *Sciaena*, *Umbrina,* "genus aff. *Umbrina*" and, more recently to *Trewasciaena*, an otolith based genus (see Schwarzhans 1993, Bannikov *et al*. 2018). The two Pannonian fossils reported herein document the earliest skeletal evidence for this genus in the fossil record. Therefore, despite their inadequate preservation, these specimens can provide some information about the potential affinities of this extinct genus. According to Bannikov *et al*. (2018), the genus *Trewasciaena* ranges from the early Miocene to the Pleistocene being restricted to fresh and brackish waters in Europe.

Sciaenid otoliths are relatively abundant in the Pannonian of the Central Paratethys (Schubert 1902, Brzobohatý & Pana 1985). Teleost otoliths, including sciaenids from the Pannonian of the Vienna Basin were summarized

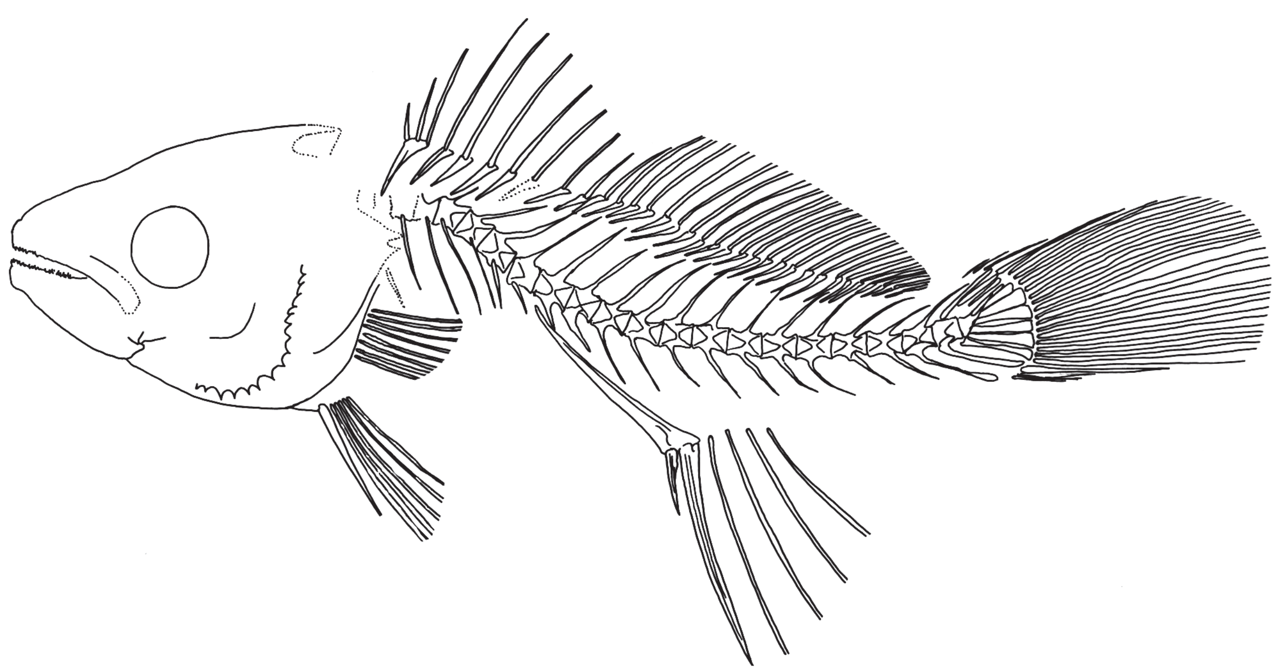

Figure 7. *Trewasciaena* cf. *kokeni* (Schubert, 1902). Reconstruction of the skeleton.

by Brzobohatý & Pana (1985) and subsequently by Schultz (2013). Nolf (2013) recognized four valid species in this area, including *Umbrina subcirrhosa* (Schubert, 1902), *U. cirrhosoides* (Schubert, 1902), "genus aff. *Umbrina*" *kokeni* (Schubert, 1902) and *Sciaena irregularis* (Koken, 1884). A more recent revision of Neogene Paratethyan sciaenids (Bannikov *et al*. 2018) confirmed the validity of the three first species, suggesting that *S. irregularis* represents an "invalid reference" for the Central Paratethys Badenian. Moreover, Bannikov *et al*. (2018) reported two other species, *Chaoia moguntiniformis* (Pana, 1977) and *Trewasciaena dobrogiaca* (Pana, 1977), both typical of the Eastern Paratethys, of which the last one invaded the Central Paratethys area toward the end of the Pannonian. Otoliths of *T. kokeni* differ from *T. suzini* Bratishko, Schwarzhans & Reichenbacher, 2015 *in* Bratishko *et al*. (2015) from the Konkian in being less elongate and having a clearly higher ostium (see Bannikov *et al*. 2018).

The stratigraphic distribution of *Umbrina subcirrhosa* is relatively wide, ranging from the Karpatian (uppermost Lower Miocene) to the Pannonian (*e.g*. Bannikov *et al*. 2018). A similar range characterizes *U. cirrhosoides*, which occurred from the basal part of the Badenian to the Middle Pontian (Portaferrian in the Dazian Basin; *e.g*. Bannikov *et al*. 2018). *Trewasciaena kokeni* represents a relatively common taxon occuring in the Central Paratethys during most of the Pannonian in Austria (*e.g*. Leobersdorf – Pannonian "B-D"; Mataschen – Pannonian "B"; Brunn a. G. and Vösendorf – Pannonian "E"; Götzendorf – Pannonian "F") and Hungary (Tihany, Fonyod – Pannonian "H"; *e.g*. Schultz 2013). Data from shallow water sediments of the younger Badenian at Děvínská Nová Ves (Slovakia, formerly "Neudorf", "Neudorf a. d. March" or "Theben Neudorf"; Schubert 1906), or from the lower Badenian at Costeiu de Sus (western Romania, Kostej in Hungarian; Schultz 2013, as *Sciaena angulata*), are based on non-figured material. The last named taxon was also mentioned from the Sarmatian of the Central Paratethys (Brzobohatý & Stancu 1974, pl. 1, fig. 5) and today is classified as a "rejected" taxon (Nolf 2013, Bannikov *et al*. 2018). *Trewasciaena kokeni* is also reported from the Mediterranean region during the late Messinian Lago-mare event (Bannikov *et al*. 2018).

The overall morphology of the specimens is in some ways reminiscent of that of the species of the genus *Umbrina*, especially the body proportions, serrated preopercle and second anal-fin spine considerably long and thick (*e.g.* Walker & Radford 1992). The genus *Umbrina* includes 17 extant species plus several otolith-based extinct species (Trewavas 1964, Gilbert 1966, Sasaki 1989, Walker & Radford 1992, Schwarzhans 1993, Nolf 2013, Bannikov *et al*. 2018, Parenti 2020). While *Trewasciaena* cf. *kokeni* shows a number of dorsal-fin spines and rays consistent with those of several species of the genus *Umbrina*, it shares the possession of a massive, greatly elongate and longitudinally striated second anal-fin spine with the Eastern Pacific species *U. analis* from which it differs in having a different number of dorsal-fin (23 *vs.* 24 to 26), anal-fin (?four *vs.* six) and pectoral-fin (probably eight *vs.* usually 17) rays, procurrent caudal-fin rays (4 + 4 *vs.* 8–9 + 7–8) and caudal vertebrae (14 *vs.* 15) (see Walker & Radford 1992).

Trewasciaena cf. *kokeni* also shows a certain degree of similarity with the extant tropical eastern Atlantic species *Pseudotolithus elongatus* in having a similar body physiognomy (*e.g.* body moderately elongate, serrated preopercle) and configuration of the anal fin, with an elongate and thick second spine that is long as the first anal-fin ray. However, these taxa can be easily separated from each other due to the different morphology of the sagittae, as well as a different number of dorsal-fin rays (23 *vs*. 29 to 34; Chao 2016). Finally, *Trewasciaena* cf. *kokeni* has a complement of dorsal-fin spines and rays similar to that of *Sciaena umbra* (11 or 12 spines and 23 to 25 rays; Chao 2016), but differs in overall habitus, morphology of the sagittae, position of mouth, distribution of teeth in the jaws, and anatomy of anal fin.

In conclusion, due to their incompleteness and juvenile nature, the two fossils described herein provide only limited information about the anatomical structure of the genus *Trewasciaena* (Fig. 7), making problematic the evaluation of its relationships within the Sciaenidae. Additional comparative information based on adult specimens would be necessary to clarify the phylogenetic position of this extinct genus that widely occurred in the fresh- and brackish waters of Europe during the Neogene.

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