Revision of the Middle Badenian fish otoliths from the Carpathian Foredeep in Moravia (Middle Miocene, Czech Republic)

by

Rostislav BRZOBOHATÝ (1) & Dirk NOLF* (2)

Abstract. – Otoliths from the Middle Miocene of the Moravian Carpathian Foredeep revealed the presence of 84 nominal species of bony fishes, as well as 22 taxa identified in open nomenclature only. Two species, *Ijimaia rara* n. sp. and *Coryphaenoides scrupus* n. sp., are described as new. The otolith assemblage is quantitatively dominated by myctophids, but stomiiforms and macrourids are significantly represented as well. Bregmacerotids, gadids and trachichthyids are common, but only represented by a single species each. The genera *Trachyscorpia*, *Serrivomer* and *Ijimaia* document the first fossil records of these taxa and the genera *Nansenia* and *Zenion* are recorded for the first time in sediments of the Paratethys. A paleobathymetric analysis of the otolith assemblages indicates water depths greater than 400 m in the depressions of the Carpathian Foredeep in Moravia. The high frequency of otoliths of *Gadiculus argenteus* supports the onset of the cold phase of the Middle Miocene Climatic Transition during the Middle Badenian. The high proportion of Recent species (~ 32%) in the otolith association of the entire Badenian of the Central Paratethys also documents the rise of modern fishes in the wider Mediterranean area since the early Middle Miocene.

Received: 22 May 2017
Accepted: 30 Nov. 2017
Editor: E. Dufour

Résumé. – Synthèse des données fournies par les otolithes de poissons Badéniens de l'avant-fosse des Carpathes moraves (Miocène moyen, République Tchèque).

L'étude des otolithes a révélé la présence de 84 espèces nominales de poissons osseux, et de 22 taxa identifiés en nomenclature ouverte. Deux espèces, *Ijimaia rara* et *Coryphaenoides scrupus,* sont nouvelles. Du point de vue quantitatif, l'assemblage est dominé par les myctophidés, et les stomiiformes et les macrouridés sont également représentés de façon significative. Les otolithes de bregmacérotidés, gadidés et trachichthyidés sont nombreuses, mais ces taxa ne sont représentés que par une seule espèce chacune. Les genres *Trachyscorpia*, *Serrivomer* et *Ijimaia* représentent la première découverte à l'état fossile de ces taxa et les genres *Nansenia* et *Zenion* représentent leur première apparition dans des sédiments de la Paratethys. Une analyse paléobathymétrique des assemblages d'otolithes indique une profondeur d'eau excédant 400 m dans les dépressions de l'avant-fosse morave. La fréquence considérable d'otolithes de *Gadiculus argenteus* illustre le début de la phase froide de la transition climatique d'âge miocène moyen au Badénien moyen. La présence de nombreuses espèces actuelles (environ 32%) dans les assemblages d'otolithes Badéniens partout dans la Paratethys centrale documente également l'apparition de poissons actuels dans l'aire méditerranéenne au sens large.

Key words
Otoliths
Middle Miocene
Langhian (Badenian)
Czech Republic
Central Paratethys

Badenian teleost otoliths of the Carpathian Foredeep in South Moravia have been studied, with interruptions, for more than 120 years. In this area, Procházka (1892a, b, c, d, 1893a, b, 1894, 1899, 1900) was the first author dealing with otoliths and using them for paleoenvironmental interpretations of some localities and regions. Unfortunately, many of his systematic data remained at the nomina nuda level. Other data on both systematics and localities were presented in the papers of Schubert (1905, 1906). In the second half of the twentieth century, Brzobohatý published a summary of systematic data on the macrourids (Brzobohatý, 1995), myctophids (Brzobohatý and Nolf, 1996, 2000), and stomiiform fishes (Brzobohatý and Nolf, 2002). Data contributing to stratigraphic, paleogeographic and paleoecologic conclusions were presented by Brzobohatý (1981, 1997, 2001), Brzobohatý and Schultz (1978) and Nolf and Brzobohatý (1994a). In the more recent years, data on otoliths were also a part of multidisciplinary studies in selected areas (Brzobohatý *in* Doláková *et al*., 2014; Brzobohatý *in* Holcová *et al*., 2016).

In the present paper, we provide a revision and new data of all otolith-based teleost taxa recorded from the Badenian in the Moravian Carpathian Foredeep, in accordance with modern taxonomy (Nolf, 2013). It provides a good addition to similar studies from the Polish Foredeep (Smigielska, 1966; Radwanska, 1992; Schwarzhans, 2010) and the Molasse of Austria (Schubert, 1906; Schultz, 2013).

Some of the figures presented have already been published by Dirk Nolf to complete his catalogue of fish otoliths (Nolf, 2013). Full data dealing with these otoliths follow in the text (see, *e.g. Serrivomer* sp., *Ijimaia rara* n. sp.)

(1) Department of Geology, Masaryk University, 61137 Brno, Kotlářská 2, Czech Republic. [rosta@sci.muni.cz]
(2) Royal Belgian Institute of Natural Sciences, rue Vautier 29, 1000 Brussels, Belgium.
* Corresponding author [dirk.nolf@scarlet.be]

GEOLOGICAL SETTING

The study area represents a relatively narrow peripheral foreland basin system of the Central Paratethys (Fig. 1). In the NW part (Czech Republic, South Moravia) its final marine stage took place at the beginning of the Middle Miocene (*i.e.* Badenian in the sense of the regional Central Paratethys stratigraphy, Fig. 2). The Badenian transgression was controlled by tectonics and eustasy and associated with basin subsidence and continuous mountain chain uplift of the Outer Carpathians during the synrift stage of back arc basin development (Kováč *et al.*, 2007). The Badenian sedimentary fill in the South Moravian Foredeep (after erosion) attains about 400 m in thickness and could have been deposited through the global sea level cycle TB 2.4 (*e.g.* Kováč *et al.*, 2007).

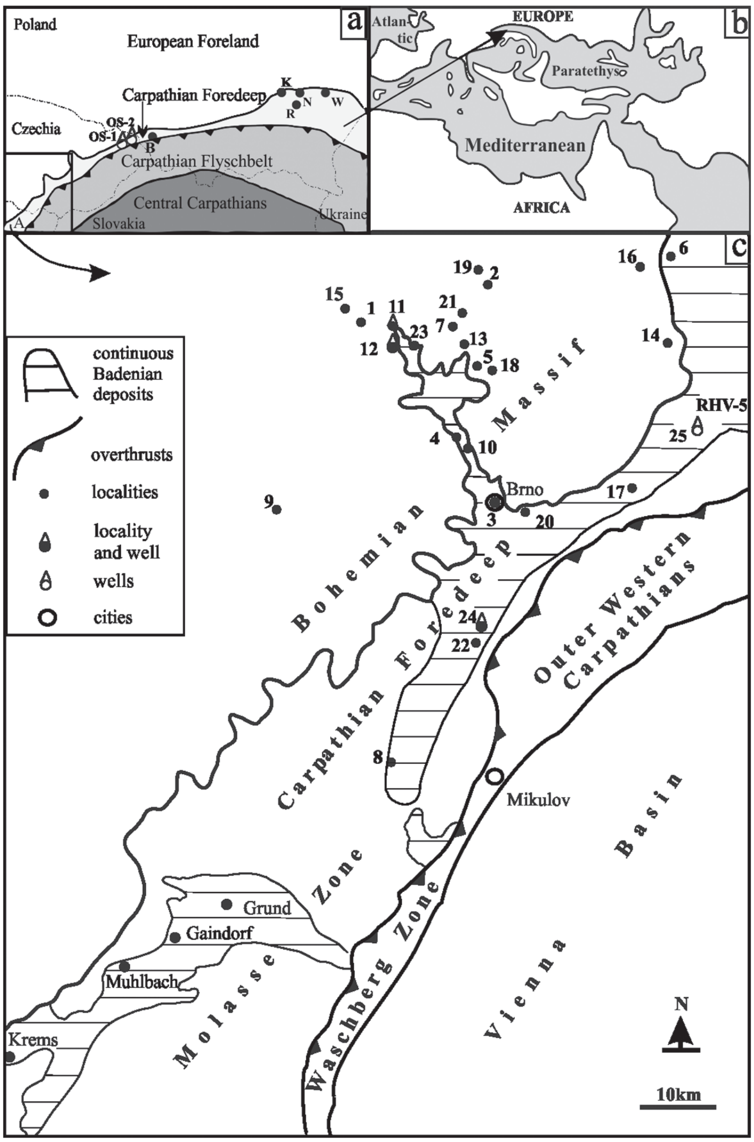

Figure 1. – Geographical (inset a), paleogeographical (inset b) and geological positions (inset c) of Middle Badenian localities. (inset a: K = Korytnica, N = Niskowa, W = Wenglinek, R = Rybnica, B = Beczyn, OS-1 = borehole OS-1 Kravaře, OS-2 = borehole OS-2 Hať, A. = Austria). (inset b: after Rögl 1998, modified). (inset c: 1 = Borač, 2 = Boskovice, 3 = Brno-Královo Pole, 4 = Čebín, 5 = Černá Hora, 6 = Drahanovice, 7 = Drnovice, 8 = Hrušovany, 9 = Kralice nad Oslavou, 10 = Kuřim, 11 = Lomnice u Tišnova, 12 = Lomnička, 13 = Lysice, 14 = Myslejovice, 15 = Nedvědice, 16 = Přemyslovice, 17 = Podbřežice, 18 = Rájec-Jestřebí, 19 = Sudice, 20 = Šlapanice, 21 = Voděrady, 22 = Žabčice, 23 = Železné, 24 = Židlochovice, boreholes Ž-1 and Ž-2, 25 = Borehole Rybníček HV-5).

At the beginning of the transgression, sands, gravels, biothermal limestones and calcareous sandstones were deposited in shallow or elevated parts of the basin, whereas unlaminated glauconitic calcareous clay (the so called "Tegel") filled the deeper parts. The formal lithostratigraphy of the basin is not yet established.

The calcareous clay is rich in fossil assemblages, *e.g.* of foraminifera, bryozoans, ostracods, molluscs, sea urchins, corals, microflora, and, last but not least, fish otoliths. Biostratigraphically, it is characterized by *Praeorbulina glomerosa circularis* (Blow) and *Orbulina suturalis* Brönnimann (Papp *et al.*, 1978). Nannoplankton, with *Helicosphaera waltrans* Theodoridis, indicates the NN 5 Zone (*e.g.* Ćorić and Švábenická, 2004). Following Hohenegger *et al.* (2014), these data allow a correlation with the middle part of the Badenian (ca 14.91~13.82 Ma), *i.e.* the upper part of the Langhian of the international scale (Fig. 2).

One of the otolith localities under investigation, Židlochovice, represents the faciostratotype of the Moravian Substage of the Badenian. It was newly drilled using two stratigraphic continuous boreholes (26 m section, roughly 14.4~13.9 Ma) and recently treated from the perspective of the multidisciplinary study (including otoliths). Cooler phases (as symptoms of the start of the Middle Miocene Climatic Transition), seasonal stratification of the water column and oscillation of the oxygen content at the bottom within a framework of subtropical climatic conditions (Doláková *et al.*, 2014) were observed in the section. The second multidisciplinary study (including otoliths) was done by Holcová *et al.* (2016) near Lomnička (20 km north of Brno). The Lomnička-1 borehole drilled through 20 m of monotonous clayey siltstones with rich microfossil assemblages. This section confirms the cyclical character of the Middle Miocene sedimentation in the area, interannual oscillations of nutrient content, symptoms of the Middle Miocene Climatic Transitions above the LO of *Helicosphaera waltrans* associated with cooling, a decrease in nutrients, a probable

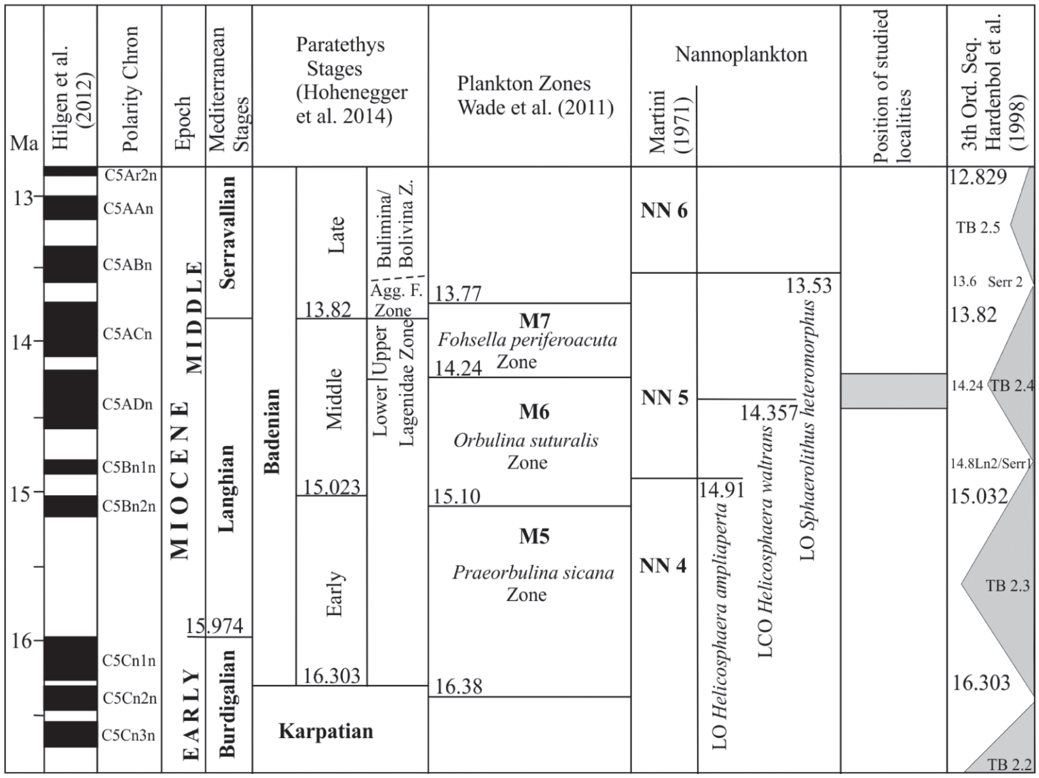

Figure 2. – Stratigraphic charts of the Badenian (after Hohenegger *et al*., 2014) and position of the localities studied.

increase of the salinity of the surface water, and an increase of seasonality.

MATERIAL AND METHODS

Calcareous clays were sampled in surface outcrops, hydrogeological samples, during excavations on several technical or industrial sites, and in three boreholes. The material from the outcrops was sampled from the sixties to the nineties of the last century. The most important samples (see Fig. 1c) are:

1. Borač – a sample of calcareous clay (210 kg) in a field, NW of the village, left side of the "Boračský potok" creek, coordinates: 49°24'42.494"N; 16°20'49.259"E. (number of taxa: 65)

2. Boskovice – excavation for a water purification station, SW part of the city, calcareous clay (70 kg), coordinates: 49°28'56.038"N; 16°38'30.565"E. (number of taxa: 8)

3. Brno-Královo Pole – an old brickyard Fy Pavlů in the city, calcareous clay (150 kg), coordinates: 49°12'53.658"N; 16°36'32.157"E. (number of taxa: 33)

4. Čebín – excavation for a house foundation, N of the village, calcareous clay (90 kg), coordinates: 49°19'9.601"N; 16°28'9.636"E. (number of taxa: 8)

5. Černá Hora – one surface sample in a field, E from the village, calcareous clay (50 kg), coordinates: 49°25'6.462"N; 16°35'16.407"E. (number of taxa: 12)

6. Drahanovice – one hydrogeological sample in the village, calcareous clay (70 kg), coordinates: 49°34'29.165"N; 17°4'34.556"E. (number of taxa: 14)

7. Drnovice – excavation for a house, NW of the village, left side of the "Úmoří" creek, calcareous clay (320 kg), coordinates: 49°28'18.841"N; 16°32'18.189"E. (number of taxa: 40)

8. Hrušovany nad Jevišovkou – excavation for the sugar factory, calcareous clay (250 kg), coordinates: 48°48'42.675"N; 16°24'5.525"E. (number of taxa: 36)

9. Kralice nad Oslavou – surface outcrop in the left bank of the "Jarošovský potok" creek, calcareous clay (50 kg), coordinates: 49°11'36.165"N; 16°12'30.349"E. (number of taxa: 9)

10. Kuřim – excavation for the petrol pump, SE of the city, calcareous clay (120 kg), coordinates: 49°17'49.065"N; 16°32'44.880"E. (number of taxa: 17)

11. Lomnička – a sample in the field, S of the village, calcareous clay (120 kg), coordinates: 49°21'54.639"N;

16°26'1.158"E. (number of taxa: 24). Borehole LOM-1: 1-20 m, coordinates: 49º23.945'N; 16º24.542'E; 382 m a.s.l. (Holcová *et al*., 2016).

12. Lomnice u Tišnova – excavation for a silo pit, S of the village, calcareous clay (210 kg), coordinates: 49°23'59.087"N; 16°24'28.466"E. (number of taxa: 31)

13. Lysice – a surface sample in a field, E of the village, calcareous clay (50 kg), coordinates: 49°27'21.787"N; 16°33'24.932"E. (number of taxa: 12)

14. Myslejovice – a hydrogeological sample, NE of the village, calcareous clay (120 kg), coordinates: 49°24'40.079"N; 17°1'58.289"E. (number of taxa: 14)

15. Nedvědice – one surface sample in the field, SE of the village, calcareous clay (50 kg), coordinates: 49°26'59.869"N; 16°20'32.062"E. (number of taxa: 3)

16. Přemyslovice – a hydrogeological sample, N of the village, calcareous clay (210 kg), coordinates: 49°33'59.491"N; 16°58'14.612"E. (number of taxa: 33)

17. Podbřežice – a sample in an old claypit, E of the village, calcareous clay (30 kg), coordinates: 49°12'42.116"N; 16°55'50.869"E. (number of taxa: 2)

18. Rájec-Jestřebí – a surface sample in a field, S of the village, calcareous clay (70 kg), coordinates: 49°24'19.682"N; 16°37'9.732"E. (number of taxa: non-identifiable fragments of myctophids)

19. Sudice – a temporary excavation, W of the village, calcareous clay (60 kg), coordinates: 49°31'44.123"N; 16°39'39.826"E. (number of taxa: 12)

20. Šlapanice – claypit of the brickyard Tondach, N of the city, calcareous clay (150 kg), coordinates: 49°10'33.126"N; 16°43'41.100"E. (number of taxa: 19)

21. Voděrady – foundations of a house, N of the village, calcareous clay (70 kg), coordinates: 49°28'44.234"N; 16°33'42.990"E. (number of taxa: 19)

22. Žabčice – one sample in an old sandpit, SW of the village, fine grained sand (50 kg), coordinates: 49°0'24.651"N; 16°35'17.177"E. (number of taxa: 15)

23. Železné – sunken road side, SW of the village, calcareous clay (120 kg), coordinates: 49°21'27.994"N; 16°26'42.239"E. (number of taxa: 9)

24. Židlochovice – an old claypit of the brickyard, NE of the city, calcareous clay (180 kg), Boreholes in the brickyard: Židlochovice Ž-1 and Ž-2, coordinates: 49°02'34"N; 16°37'30"E. Z = 219-240 m (Doláková *et al*., 2014). (number of taxa: 22)

25. Borehole Rybníček HV-5: 0-205 m (see Brzobohatý, 1981).

The otoliths were studied from washed residues (fraction 0.063-2.0 mm) and examined using a Wild Heerbrugg microscope. Borehole sections were sampled for otoliths every meter. The paleobathymetry of each sample was estimated using the method proposed for otoliths by Nolf and Brzobohatý (1994a). All otolith-based Badenian species from the Carpathian Foredeep in Moravia are listed, and the new ones or those subject to comments are figured.

Data from the locality Mikulov, Kienberg, published by Brzobohaty *et al*. (2007), are not included here. Although the town of Mikulov is indicated in our Fig. 1, the Kienberg site, some km east of the town, is located in the Vienna Basin, and not in the Carpathian Foredeep. The Kienberg site provided a diversified neritic fauna of 63 species including many near-shore taxa that are unknown in the Carpathian Foredeep.

SYSTEMATIC PALEONTOLOGY

The classification used is the one of Nelson (2006), also used by Nolf (2013).

Remarks on taxa requiring comments

***Serrivomer* sp.** (Pl. 1, Fig. 2a, b) (see also Nolf, 2013: pl. 29, illustration only). One perfectly preserved otolith from Lomnička (Badenian) of pear-like shape, with a relatively narrow sulcus, blunt and short protruding salient ostial colliculum clearly belongs to a *Serrivomer*. Otoliths of only three nominal present-day species are known: *S. beanii* Gill and Ryder, 1883, *S. samoensis* Bauchot, 1959 and *S. sector* Garman, 1899. Our specimen matches best with otoliths of the latter, Pacific species (see Rivaton and Bourret, 1999, pl. 86, fig. 5; Nolf, 1985: fig. 38E). However, the variability of this Recent species seems to be considerable and some specimens differ markedly in shape (comp. Rivaton and Bourret, 1999, pl. 86, figs 6-11). The otolith of a Recent *Serrivomer* sp., figured by Smale *et al*. (1995: pl. 5, fig. E1), also shows very similar features, but it is markedly longer (index L:H = 1.8). Otoliths of *S. samoensis* (see Nolf, 2013: pl. 29) and *S. beanii* (see Smale, 1995: pl. 5, fig. D1 and 2; Campana, 2004: pl. 25) show many more differences from the Badenian specimen. The fossil material does not allow a more precise allocation, but this specimen represents the only fossil record of the genus *Serrivomer* and the family Serrivomeridae.

***Sarmatella* aff. *pulchra* (Smigielska, 1966)** (Pl. 1, Fig. 7a, b). A small clupeid otolith with a narrow, but prominent rostrum seems to be closely related or identical with those described as *Clupea pulchra* from the Badenian of Poland by Smigielska, and interpreted as an incertae sedis clupeid at generic level by Nolf (2013: p. 40). Recently, Baykina and Schwarzhans (2016) described a skeleton of *Sarmatella doljeana* (Kramberger, 1883), with an otolith *in situ*, from the Sarmatian of Beograd (Serbia), as well as osteological material of *Sarmatella tsurevica* (Baykina, 2012) from the early Sarmatian of the Northern Caucasus with an otolith supposed to be associated with bones of that species. On the basis of the similarity of the otoliths of both these

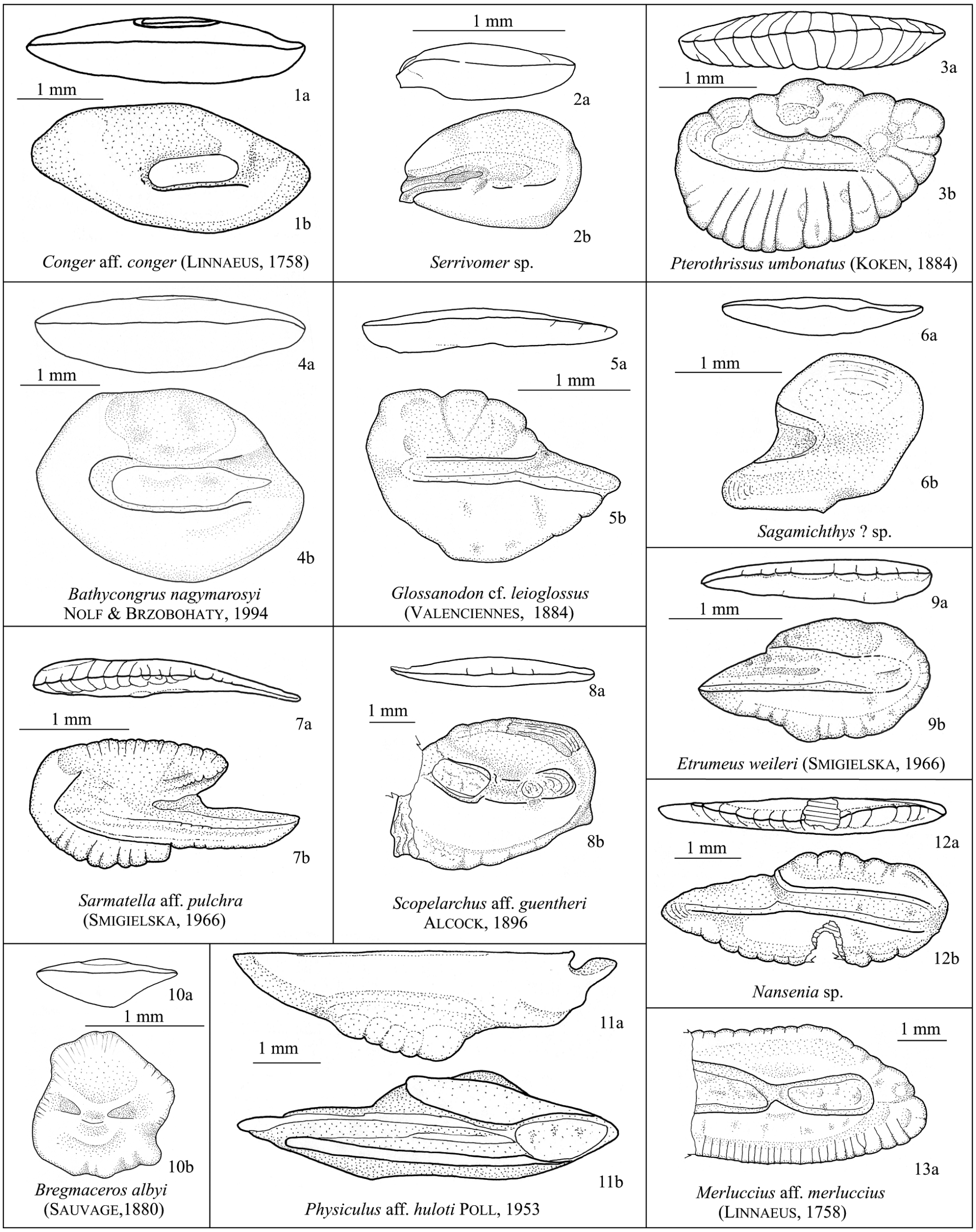

Plate 1. – Explanation of the plates: All figured specimens are deposited in the collections of the Department of Geological Sciences, Masaryk University (DGS MU), Brno, Kotlářská 2, Czech Republic. The fossil otoliths bear numbers of the collection of types and figured fossil fish specimens in the DGS MU (Inv. Nr. O 315-377). The annotations a, b and c are used to indicate ventral, inner (= mesial) and posterior views, respectively. Figures with only numbers and no letter show inner views. In the captions, L stands for left otolith and R for right otolith. **1**: *Conger* aff. *conger* (Linnaeus, 1758); Drnovice, Badenian, L (DGS MU Inv. Nr. O 315). **2**: *Serrivomer* sp.; Lomnička, Badenian, R (DGS MU Inv. Nr. O 316). **3**: *Pterothrissus umbonatus* (Koken, 1884); Drnovice, Badenian, R (DGS MU Inv. Nr. O 317). **4**: *Bathycongrus nagymarosyi* Nolf & Brzobohaty, 1994; Voděrady, Badenian, R (DGS MU Inv. Nr. O 318). **5**: *Glossanodon* cf. *leioglossus* (Valenciennes, 1848); Lomnice u Tišnova, Badenian, R (DGS MU Inv. Nr. O 319). **6**: *Sagamichthys* ? sp.; Voděrady, Badenian, R (DGS MU Inv. Nr. O 320). **7**: *Sarmatella* aff. *pulchra* (Smigielska, 1966); Lomnice u Tišnova, Badenian, L (DGS MU Inv. Nr. O 321). **8**: *Scopelarchus* aff. *guentheri* Alcock, 1896; Hrušovany nad Jevišovkou, Badenian, R (DGS MU Inv. Nr. O 326). **9**: *Etrumeus* ? *weileri* (Smigielska, 1966); Borač, Badenian, R (DGS MU Inv. Nr. O 323). **10**: *Bregmaceros albyi* (Sauvage, 1880); Lomnice u Tišnova, Badenian, R (DGS MU Inv. Nr. O 324). **11**: *Physiculus* aff. *huloti* Poll, 1953; Lomnice u Tišnova, Badenian, L (DGS MU Inv. Nr. O 325). **12**: *Nansenia* sp.; Borač, Badenian, L (DGS MU Inv. Nr. O 322). **13**: *Merluccius* aff. *merluccius* (Linnaeus, 1758); Lomnice u Tišnova, Badenian, L (DGS MU Inv. Nr. O 327).

species and those of the clupeid described by Smigielska, he attributed the latter species to the extinct genus *Sarmatella*.

***Arius* aff. *germanicus* (Koken, 1891)** (Pl. 5, Fig. 1a, b). Ariids are very rare in the Miocene record despite their robust utricular otoliths. There are three taxa mentioned from the Miocene of the Paratethys basins. A single adult and well-preserved specimen from Lomnice u Tišnova (L = 11.8 mm, H = 10.0 mm, L:H = 1.18) differs from otoliths described from the Badenian of Romania as *A. germanicus* by Weiler (1950: pl. 1, fig. 1) in the more compressed appearance only. It seems to be very close to the Oligocene otoliths of *A. germanicus*, especially to the Lower Oligocene ones (comp. also Koken's, 1891 descriptions: p. 81), but it differs in the more compressed appearance and more rounded dorsal margin from the Middle Oligocene specimen (Koken, 1891: pl. 1, fig. 3a, b, c; Nolf, 2013: pl. 37). A comparison with *A. nucleus* (Weinfurter, 1952: p. 488, pl. 5, figs 1, 2) and "genus *Ariidarum*" sp. (Radwańska, 1992: pl. 4, fig. 15) from the Badenian of the Styrian Basin and Carpathian Foredeep of Poland, respectively, reveals many more differences.

***Glossanodon* cf. *leioglossus* (Valenciennes, 1848)** (Pl. 1, Fig. 5a, b). A perfectly preserved otolith from Lomnička (length = 2.5 mm; height = 1.6 mm) could be conspecific with the present-day species *G. leioglossus*, but more material is required for an unambiguous specific identification. This Eastern Atlantic fish (including the Western Mediterranean and southern part of the Adriatic Sea) can be found near the bottom on the outer shelf and upper slope (Jardas, 1996). *G.* cf. *leioglossus* represents the first otolith-based fossil record of the genus, but skeletons of the fossil *G. musceli* (Paucá, 1929) are relatively abundant in the Lower Oligocene of the Carpathians (*e.g.* Kotlarczyk *et al.*, 2006).

***Nansenia* sp**. (Pl. 1, Fig. 12a, b). Otoliths of the genus *Nansenia* are rare in the European Neogene and are usually mentioned as *Nansenia* sp. (Nolf and Steurbaut, 1983; Schwarzhans, 1986; Nolf and Cappetta, 1989). The Badenian otoliths (Borač: 2 specimen; Drnovice: 3 specimens) could be conspecific with the ones from the Mediterranean Lower Pliocene (Nolf and Cappetta, 1989: pl. 3, figs 13-14). Both have a straight dorsal margin with rounded wave-like curves and a rather prominent anterodorsal angle. The same feature can be found in the fragmentary specimen of *Nansenia* sp. from the Mediterranean Tortonian (Nolf and Steurbaut, 1983: pl. 1, fig. 13). This feature differentiates the Badenian otoliths from those of the Recent *N. groenlandica* (Reinhardt, 1840) (compare, *e.g.* Nolf and Steurbaut, 1983: pl. 1, fig. 12; Nolf, 2013: pl. 41), which is also reported from the Mediterranean Gelasian in Greece (and associated with a cold event; Agiadi *et al.*, 2010, 2011) and the Pleistocene in Italy (Girone, 2003; Girone *et al.*, 2006) and the Indo-Pacific *N. ardesiaca* Jordan and Thompson, 1914 (Ohe, 1985: p. 45, fig. 27). This feature, however, seems to vary in *N. macrolepis* (Gilchrist, 1922) – see Smale *et al.* (1995: pl. 9, fig. D1-2) and in the *Nansenia* sp. figured by Rivaton and Bourret (1999: pl. 88, figs 1-4). More and well-preserved fossil otoliths and data on Recent species are required to make more precise taxonomic conclusions.

The genus *Nansenia* includes foremost oceanic bathyphile pelagic fishes. *Nansenia iberica* Matallano, 1985 and *N. oblita* (Facciola, 1887), *e.g.* both also living in the Mediterranean, are mesopelagic. At present, *N. groenlandica* lives in deep waters (up to 1400 m) in the North Atlantic and the Western Indian Ocean (Froese and Pauly, 2016). The present fossil record is the first one of the genus in the Paratethys.

***Sagamichthys* ? sp**. (Pl. 1, Fig. 6a, b). An otolith of a juvenile fish from Voděrady (L = 1.8 mm; H = 1.2 mm; L:H = 1.5) represents an alepocephalid fish. Its general morphology and sulcus show similarities with those of the present-day species *Persparsia kopua* (Phillips, 1942) – see Smale *et al.* (1995: pl. 10, fig. G1) – and with *Sagamichthys abei* Parr, 1953 (Nolf, 2013: pl. 42). The former species is a mesopelagic fish distributed everywhere in the southern hemisphere (excluding South America) in the depth range of 700 to 1500 m, whereas the latter lives in the Pacific. In comparison with the Eastern Atlantic (see Smale *et al.*, 1995: pl. 10, figs H, I) and Tortonian (Lin *et al.*, 2015: pl. 2, fig. 4) *S. schnakenbecki* (Krefft, 1953), the Badenian specimen is clearly oblique along a praeventral-postdorsal axis. Otoliths of the West Indian *S. gracilis* Sazov, 1978, are unknown. The available fossil material does not allow any more precise systematic conclusions.

***Scopelarchus* aff. *guentheri* Alcock, 1896** (Pl. 1, Fig. 8a, b). An adult *Scopelarchus* otolith from Hrušovany nad Jevišovkou is well preserved, but damaged at the anterodorsal part; a second juvenile one from Židlochovice is somewhat eroded. The main features of these otoliths are the clearly divergent dorsal and ventral margins, an oblique anterior margin and a relatively small L/H index (1.3). The ostial colliculum is large; the cauda is elongated and narrowing towards the anterodorsal angle. These features are different from the Oligocene and Lower Miocene species *S. nolfi* Steurbaut, 1982 (*e.g.* Nolf and Brzobohatý, 1994b: pl. 4, figs 1-6) and from the Recent *S. analis* (Brauer, 1902), also known from the Mediterranean Pliocene and Pleistocene (Nolf and Cappetta, 1989; Girone *et al.*, 2006). The otoliths are most similar to the present-day *S. guentheri* (see Rivaton and Bourret, 1999: pl. 129, figs 17-20). Additional and better-preserved material is required to decide about the precise specific affinity of the Badenian otoliths. Scopelarchids seem to be very rare in the Miocene of the Paratethys in contrast to the Oligocene Kiscell Clay and Pouzdřany Formation (Nolf and Brzobohatý, 1994b; Brzobohatý and Krhovský, 1998). In the Recent fauna, *S. guentheri* lives mesopelagically (in the upper 150 m at night), mainly in tropical areas of the eastern Atlantic and the Indo-Pacific (Froese and Pauly, 2016).

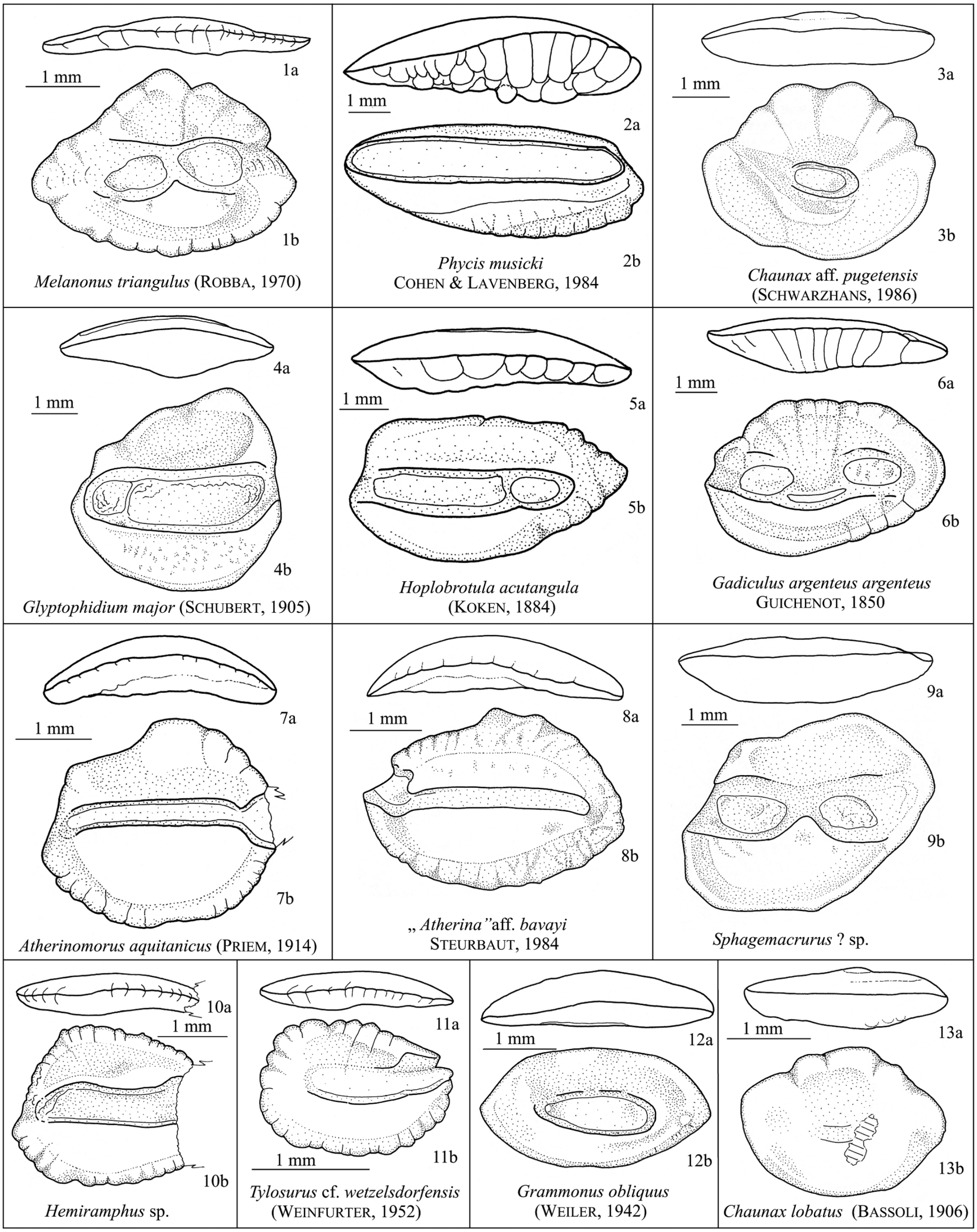

Plate 2. – **1**: *Melanonus triangulus* (Robba, 1970); Brno-Královo Pole, Badenian, L (DGS MU Inv. Nr. O 328). **2**: *Phycis musicki* Cohen & Lavenberg, 1984; Borač, Badenian, L (DGS MU Inv. Nr. O 329). **3**: *Chaunax* aff. *pugetensis* (Schwarzhans, 1986); Drnovice, Badenian, R (DGS MU Inv. Nr. O 336). **4**: *Glyptophidium major* (Schubert, 1905); Drnovice, Badenian, L (DGS MU Inv. Nr. O 331). **5**: *Hoplobrotula acutangula* (Koken, 1884); Borač, Badenian, R (DGS MU Inv. Nr. O 332). **6**: *Gadiculus argenteus argenteus* Guichenot, 1850; Drnovice, Badenian, R (DGS MU Inv. Nr. O 333). **7**: *Atherinomorus aquitanicus* (Priem, 1914); Lomnice u Tišnova, Badenian, R (DGS MU Inv. Nr. O 334). **8**: „*Atherina*" aff. *bavayi* (Steurbaut, 1984); Lomnice u Tišnova, Badenian, R (DGS MU Inv. Nr. O 335). **9**: *Sphagemacrurus* ? sp.; Drnovice, Badenian, R (DGS MU Inv. Nr. O 330). **10**: *Hemiramphus* sp.; Lomnice u Tišnova, Badenian, L (DGS MU Inv. Nr. O 337). **11**: *Tylosurus* cf. *wetzelsdorfensis* (Weinfurter, 1952); Borač, Badenian, L (DGS MU Inv. Nr. O 338). **12**: *Grammonus obliquus* (Weiler, 1942); Hrušovany nad Jevišovkou, Badenian, R (DGS MU Inv. Nr. O 339). **13**: *Chaunax lobatus* (Bassoli, 1906); Borač, Badenian, R (DGS MU Inv. Nr. O 340).

***Sphagemacrurus* ? sp**. (Pl. 2, Fig. 9a, b). A single and perfectly preserved macrourine otolith from Drnovice (L = 4.4 mm; H = 3.3 mm; L:H = 1.3), with a strongly developed posterodorsal part. Its features, such as a strong posterodorsal expansion, the regular collicula, the absence of a collicular crest, and a smooth and flat ventral field with a relatively wide ventral furrow, show affinities with otoliths of the Indo-West Pacific *Sphagemacrurus richardi* (Weber, 1913) (Nolf and Steurbaut, 1989: pl. 4, fig. G), which seem to be more extended in the dorso-ventral direction. Otoliths of the West Atlantic *S. hirundo* (Collett, 1896) have a higher and robust posterodorsal part as well as a deeper ventral rim (Schwarzhans, 2013: pl. 16, fig. 13). More fossil material is required for an adequate taxonomic determination.

***Melanonus triangulus* (Robba, 1970)** (Pl. 2, Fig. 1a, b). This species is relatively rare in the Moravian Badenian (see Tab. IC), but some of the otoliths are perfectly preserved and there is no doubt about the presence of *M. triangulus* in the Middle Badenian Sea. *Melanonus triangulus* occurs from the Lower Oligocene (Nolf and Steurbaut, 1988; Brzobohatý and Krhovský, 1998 – both as *M. gabbai*) to the Upper Miocene of the Mediterranean (Robba, 1970: pl. 11, figs 7, 8, pl. 12, figs 1-3; Nolf and Steurbaut, 1983: pl. 3, figs 20, 21). Otoliths of this species show very close relationships with those of the Recent *M. zugmayeri* Norman, 1930 (*e.g.* Nolf and Steurbaut, 1983: pl. 4, fig. 1; Nolf, 1985: fig. 49 O; Smale *et al.*, 1995: pl. 28, fig. C1; Campana, 2004: pl. 67). The juvenile and damaged specimen from the Burdigalian of the Aquitaine Basin, illustrated by Nolf and Brzobohatý (2002: pl. 7, fig. 6), may also belong to *M. triangulus*. A second present-day species of the genus, *M. gracilis* Günther, 1878, differs markedly from *M. triangulus* by the irregular outline of the otoliths (Nolf and Steurbaut, 1983: pl. 4, fig. 2-7). Two other fossil species, the Paleocene/Eocene *M. ellesmerensis* Schwarzhans, 1986 and the Pliocene *M. paralyconus* Schwarzhans, 1986 also present a significantly different outline. In the Recent fauna, *Melanonus* is widespread (Atlantic, Indian Ocean and Pacific, tropical to temperate or sub Antarctic waters) in deep-water (oceanic, meso- to bathypelagic).

***Chaunax* aff. *pugetensis* (Schwarzhans, 1986)** (Pl. 2, Fig. 3a, b). In the Badenian of the Carpathian Foredeep, chaunacid otoliths are very rare and are represented mainly by juvenile specimens, not diagnostic at species level. Two otoliths from Drnovice can be compared with the Pliocene species *Ch. pugetensis* (Schwarzhans, 1986: pl. 5, figs 55, 56). The Moravian specimens are slightly different from the Pliocene otoliths in their somewhat higher form, the more backwards shifted dorsal tip and a wider and flatter ventral furrow. Other known species of *Chaunax* from the Paratethys are *Ch. niederleisensis* (Schubert, 1906) from the Badenian of the Vienna Basin, which is known from the holotype only (see Nolf, 1981, 2013: pl. 146), and *Chaunax* sp. from the Badenian Korytnica Clay in Poland (Radwańska, 1992: pl. 7, fig. 6). In the Recent fauna, the genus includes mainly bathydemersal deep-water fishes in the Atlantic and the Indo-Pacific, but it is absent from the Mediterranean.

***Zenion hololepis* (Goode & Bean, 1896)** (Pl. 3, Fig. 9a, b). Only a single and relatively well preserved specimen from Borač (L = 1.8 mm; H = 1.45 mm; L:H = 1.24) shows typical, but subadult features of otoliths of the *Zenion* group (sensu Nolf and Tyler, 2006), especially *Z. hololepis* (*e.g.* Smale *et al.*, 1995: pl. 45, figs C1, C2; Nolf and Tyler, 2006: pl. 4, fig. 6). The oldest record of this species is from the Mediterranean Pliocene (SE France, Le-Puget-Sur-Argens; Nolf and Cappetta, 1989: pl. 14, figs 12, 13; Schwarzhans, 1986: pl. 2, fig. 18 – in the last case as *Zenion* sp.). The genus *Zenion* has already been recognized from the Lower Oligocene of northern Italy (*Z.* sp., Nolf and Steurbaut, 2004: pl. 9, fig. 2). Otoliths of two other Recent species of the genus, *Z. japonicus* Kamohara, 1934 (Nolf, 1985: pl. 55B, 2013: pl. 173; Nolf and Tyler, 2006: pl. 4, fig. 1) and *Z. longipinnis* Kotthaus, 1970 (Rivaton and Bourret, 1999: pl. 144, figs 1-2; Nolf and Tyler, 2006: pl. 4, fig. 7), differ at first glance from those of *Z. hololepis* by their shape. Otoliths of the Recent Indo-Pacific species *Z. leptolepis* (Gilchrist and von Bonde, 1924) are not known. The Moravian record is the first indication of the presence of *Zenion* in the Miocene of the Central Paratethys and adds new data to the poorly known paleogeography of these fishes.

A list of the otolith-based fossil record of zeiforms was given by Nolf and Tyler (2006). Today, *Z. hololepis* belongs to the bathydemersal fauna of the Atlantic and the Indo-Pacific, where it lives between 180 and 650 m, but it does not occur in the Mediterranean.

***Trachyscorpia* aff. *cristulata* (Goode and Bean, 1896)** (Pl. 5, Fig. 6a, b) A single, large (L = 20.0 mm, H = 10.5 mm, T = 4.0 mm; OL:OH = 1.9), well-preserved and strongly compressed otolith from Brno-Královo Pole is larger than the known otoliths of the extant species of the genus (IRSNB collection; Smale *et al.*, 1995: pl. 51, fig. A1-3). Its dorsal rim is convex and roughly undulated without prominent angles; the ventral rim is regularly concave. The posterior end is largely blunt and short; the rostrum is long and acuminate. There is no antirostrum or excisura. The inner face is markedly convex, ventrally much higher than dorsally, with a prominent morphology. The dorsal area is flat; the ventral area is high, with a deep and wide ventral furrow. The sulcus is deep and wide, unclearly divided, with unregularly spread colliculum. The ostium is shallower and shorter than the cauda, slightly curved dorsally, unclearly opened anteriorly. The outer face is flat with five distinct radial furrows and irregular bumps.

There are six extant species of this genus of marine deep-water scorpionfishes, living below 200 m. The Badenian specimen is rather similar to the otoliths from the East

Table Ia-e. – List of teleost species represented by otoliths in the Badenian of the Carpathian Foredeep in South Moravia [B1986 = Brzobohatý (1986); B1995 = Brzobohatý (1995); BN1996 = Brzobohatý and Nolf (1996); BN2000 = Brzobohatý and Nolf (2000); BN2002 = Brzobohatý and Nolf (2002); HBKN2016 = Holcová *et al*. (2015); Sch1906 = Schubert (1906)]. For number of localities see Chapter 3 of the Material and methods.

Taxa		Alpine-Carpathian Foredeep (Molasse)																									
		Moravia																								Lower Austria	Poland
		Localities (number of specimens, this paper)																									
* taxa mentioned in section 4.1	Iconography	1 Borač	2 Boskovice	3 Brno	4 Čebín	5 Cerná Hora	6 Drahanovice	7 Drnovice	8 Hrušovany	9 Kralice n. O.	10 Kurim	11 Lomnice	12 Lomnička	13 Lysice	14 Myslejovic.	15 Nedvědice	16 Přemyslov.	17 Podbřežice	18 Rájec-Jestř.	19 Sudice	20 Šlapanice	21 Voděrady	22 Žabčice	23 Železné	24 Židlochov.		
ALBULIDAE																											
Pterothrissus umbonatus (Koken, 1884)	Pl. 1, Fig. 3	8														1											P
CONGRIDAE																											
Ariosoma balearicum (Delaroche, 1809)	Pl.5, Fig. 2			2																							P
Bathycongrus nagymarosyi Nolf & Brz. 1994	Pl. 1, Fig .4			1																							
Conger aff. *conger* (Linnaeus, 1758)	Pl. 1, Fig. 1							1																			P
Rhynchoconger pantanellii (Bassoli & S., 1906)	Pl. 5, Fig. 12	1																									P
SERRIVOMERIDAE																											
Serrivomer sp.	Pl .1, Fig. 2												1														
CLUPEIDAE																											
Etrumeus weileri (Smigielska, 1966)	Pl. 1, Fig. 9	10																							2		P
**Sarmatella* aff. *pulchra* (Smigielska, 1966)	Pl. 1, Fig. 7	5										7															P
ARIIDAE																											
**Arius* aff. *germanicus* Koken, 1884	Pl. 5, Fig. 1											1															
ARGENTINIDAE																											
**Glossanodon cf. leioglossus* (Valen., 1848)	Pl. 1, Fig. 5												1														
MICROSTOMATIDAE																											
**Nansenia* sp.	Pl. 1, Fig. 12	2						3																			
ALEPOCEPHALIDAE																											
**Sagamichthys*? sp.	Pl. 1, Fig. 6																					1					
Xenodermichthys aff. *copei* (Gill, 1884)	B1986 (Pl. 1, Fig. 1-3)	14							1								1										
GONOSTOMATIDAE																											
Bonapartia pedaliota Goode & Bean, 1896	HBKN2016 (Textfig. 9A)												1														
Bonapartia sp.	BN2002 (Pl. 1, Fig. 3-5)	6		2				10				5	1							3							
"Gonostoma" aff. *hoffmani* (N. & B., 2003)	BN2002 (Pl. 2, Fig. 5)	4									1																
STERNOPTYCHIDAE																											
Maurolicus muelleri (Gmelin, 1789)	BN2002 (Pl. 1, Fig. 17-19)	20				1		3					40				4			1		1					
Valenciennellus tripunctulatus (Esmark, 1871)	BN2002 (Pl. 1, Fig. 10-15)	39				1		22	6					3	9		7			1		1			4		P
Valenciennellus sp.	BN2002 (Pl. 1, Fig. 16)	1																									
Polyipnus sp.	BN2002 (Pl. 2, Fig. 14)	1																									
PHOSICHTHYIDAE																											
Vinciguerria poweriae (Cocco, 1838)	BN2002 (Pl. 2, Fig. 6-10)	143				30		349	12			135					65			14		53					
Phosichthys sp.	BN2002 (Pl. 2, Fig. 13)										1																
Woodsia emi Brzobohaty & Nolf, 2002	BN2002 (Pl. 2, Fig. 16-17)							1	1																		

Table I. Continued.

Taxa		Alpine-Carpathian Foredeep (Molasse)																									
		Moravia																								Lower Austria	Poland
		Localities (number of specimens, this paper)																									
* taxa mentioned in section 4.1	Iconography	1 Borač	2 Boskovice	3 Brno	4 Čebín	5 Cerná Hora	6 Drahanovice	7 Drnovice	8 Hrušovany	9 Kralice n. O.	10 Kurim	11 Lomnice	12 Lomnička	13 Lysice	14 Myslejovic.	15 Nedvědice	16 Přemyslov.	17 Podbřežice	18 Rájec-Jestř.	19 Sudice	20 Šlapanice	21 Voděrady	22 Žabčice	23 Železné	24 Židlochov.		
STOMIIDAE																											
Astronesthes? sp.	BN2002 (Pl. 2, Fig. 11-12)		2						1				1														
ATELEOPODIDAE																											
Ijimaia rara n. sp.	Pl. 5, Fig. 7	1																									
SCOPELARCHIDAE																											
**Scopelarchus* aff. *guentheri* Alcock, 1896	Pl. 1, Fig. 8								1																		
MYCTOPHIDAE																											
Benthosema fitchi Brzobohaty & Schultz, 1978	BN1996 (Pl. 1, Fig. 5-6)	4		45			52	18	9		10				31		35						2	1	5	LA	P
Diaphus acutirostrum (Holec, 1975)	BN2000 (Pl. 3, Fig. 1-6)	246		61	10	3	15	307	70			55	32	3	2		11			1	3	70	5		31	LA	
D. cahuzaci Steurbaut, 1979	BN2000 (Pl. 5, Fig. 1-6)	16	6	94	1	7	46	112	11	45	7	5	4		16		140			1	7	34	5	25	8	LA	P
D. debilis (Koken, 1891)	BN2000 (Pl. 2, Fig. 13-18)	58	1	37	9	19	79	267	50	11	11	33	161	1	3		139			5	15	90		51	15	LA	P
D. haereticus (Brzobohaty & Schultz, 1978)	BN2000 (Pl. 1, Fig. 1-14)	14	5	52	1			30	2		1		6				9			1	6	18	10	4	5	LA	
D. kokeni (Prochazka, 1893)	BN2000 (Pl. 2, Fig. 1-6)	6	65		1		3	73	8	4	8	4			1		17				23	8	1	9	3		P
D. metopoclampoides Steurbaut, 1983	BN2000 (Pl. 4, Fig. 7-14)			1																	2					LA	
D. regani Taaning, 1928	BN2000 (Pl. 3, Fig. 11-14)	39	1	2	1	2		152	28	5	5						21				15	4		1	15	aff.	aff.
D. taaningi Norman, 1930	BN2000 (Pl. 2, Fig. 7-12)	25		28		2	33	15	1	7		6	1		4		24			2	3	11	8		12	LA	
Hygophum hygomii (Lütken, 1892)	BN1996 (Pl. 2, Fig. 1-24)			13					2		5				1		1					3					aff.
H. murbani (Weinfurter, 1952)	BN1996 (Pl .3, Fig. 7-8)			2			3	3	3			1					1										P
Lampadena gracile (Schubert, 1912)	BN1996 (Pl. 4, Fig. 1-6)			4			1				1						21										P
L. speculigeroides Brzobohaty & Nolf, 1996	BN1996 (Pl. 4, Fig. 12-16)							1															3				
Lampichthys schwarzhansi Brzobohaty, 1986	B1986 (Pl. 2, Fig. 4-12)	6		30			7		2		1				3		5				1		1		1	LA	P
Notoscopelus mediterraneus (Koken, 1891)	BN1966 (Pl. 8, Fig. 1-8)	5		9	1	1	3	34	30			7	6	1			9				5	10	2				
Symbolophorus meridionalis Steurbaut, 1979	BN1996 (Pl. 8, Fig. 9-15)								1				1		1												
Myctophidae indet. (corroded and broken specimens, < *Diaphus*)		~10.000	50	~3.500	200	300	700	~2.000	~2.000	350	300	~2.000	~1.000	200	70	6	~5.000	1	100	100	220	300	12	300	~1.000	LA	P
BREGMACEROTIDAE																											
Bregmaceros albyi (Sauvage, 1880)	Pl. 1, Fig. 10	96						3	1			3				1					5					LA	
MACROURIDAE																											
Bathygadus novus (Bassoli, 1906)	B1995 (Pl. 1, Fig. 12, 13)			1																							
Gadomus tejkali (Brzobohaty & Schultz, 1978)	B1995 (Pl. 1, Fig. 1-11)	170		8			3	32	14		1	1	2		3		8			1	10	2		3		LA	P
Coelorinchus arthaberi (Schubert, 1905)	B1995 (Pl. 1, Fig. 17-18)								2								1										
C. caelorhinchus (Risso, 1810)	B1995 (Pl. 2, Fig. 3-6)	3		6					4																		
C. aff. cristatus (Bassoli, 1906)	B1995 (Pl. 3, Fig. 6-8)	3																									
C. macruruloides Brzobohaty, 1986	B1995 (Pl. 2, Fig. 8-12)	38		8				9	3			1	2				1				2		2				
Coryphaenoides gaemersi Brzobohaty, 1986	B1995 (Pl. 4, Fig. 4)			1					1																		

Table I. Continued.

Taxa		Alpine-Carpathian Foredeep (Molasse)																									
		Moravia																									
		Localities (number of specimens, this paper)																									
* taxa mentioned in section 4.1	Iconography	1 Borač	2 Boskovice	3 Brno	4 Čebín	5 Cerná Hora	6 Drahanovice	7 Drnovice	8 Hrušovany	9 Kralice n. O.	10 Kurim	11 Lomnice	12 Lomnička	13 Lysice	14 Myslejovic.	15 Nedvědice	16 Přemyslov.	17 Podbřežice	18 Rájec-Jestř.	19 Sudice	20 Šlapanice	21 Voděrady	22 Žabčice	23 Železné	24 Židlochov.	Lower Austria	Poland
C. kalvodai Brzobohaty, 1995	B1995 (Pl. 4, Fig. 5-7)	2		4																							
C. scrupus n. sp.	Pl. 5, Fig. 13-14													3													
Macrouroides kokeni (Rzehak, 1893)	B1995 (Pl. 3, Fig. 1- 4)			1																							
Nezumia aequalis (Günther, 1878)	B1995 (Pl. 5, Fig. 1-5)	17		5					20												1	1					
N. ornata (Bassoli, 1906)	B1995 (Pl. 5, Fig. 6,7)	3							7			13								1	1	8					?P
**Sphagemacrurus* ? sp.	Pl. 2, Fig. 9							1																			
Trachyrincus scabrus (Rafinesque, 1810)	Pl. 5, Fig. 4			134																	1		1		3		
MORIDAE																											
Physiculus aff. *huloti* Poll, 1953	Pl. 1, Fig. 11	20							11			3	2				1					1			2		P
MELANONIDAE																											
**Melanonus triangulus* (Robba, 1970)	Pl. 2, Fig. 1	5		1					2								1										
MERLUCCIDAE																											
Merluccius aff. *merluccius* (Linnaeus, 1758)	Pl. 1, Fig. 13			4								3					1								1		P
PHYCIDAE																											
Phycis musicki Cohen & Lavenberg, 1984	Pl. 2, Fig. 2	5																								LA	P
GADIDAE																											
Gadiculus argenteus argenteus Guichen., 1850	Pl. 2, Fig. 6	151		22		1	18	485	17	3		72	30	1	4	1	81				15	16	1	4		LA	P
OPHIDIIDAE																											
Glyptophidium major (Schubert, 1905)	Pl. 2, Fig. 4	11		5				12				1		1			1										
Hoplobrotula acutangula (Koken, 1884)	Pl. 2, Fig. 5	5						1				1															P
BYTHITIDAE																											
„ aff. *Dermatopsis*" *boratschensis* (Sch., 1906)	Sch1906(Pl. 19, Fig. 27, 28)	18					1							3													
Grammonus obliquus (Weiler, 1942)	Pl. 2, Fig. 12			1				1	3		3	1	1	1			2								2		P
"*Bythites*" *occultoides* (Schubert, 1906)	Sch1906(Pl. 19, Fig. 57, 58)	2																									
CHAUNACIDAE																											
Chaunax lobatus (Bassoli, 1906)	Pl. 2, Fig. 13	3												2													
**Ch.* aff. *pugetensis* (Schwarzhans, 1986)	Pl. 2, Fig. 3							2																			
ATHERINIDAE																											
Atherina austriaca Schubert, 1906	Nolf, 2013 (Pl. 151)	8						2																			?
Atherinomorus aquitanicus (Priem, 1914)	Pl. 2, Fig. 7	3										2															P
"*Atherina*" aff. *bavayi* Steurbaut, 1984	Pl. 2, Fig. 8										1																
HEMIRAMPHIDAE																											
Hemiramphus sp.	Pl. 2, Fig. 10	1										1															
BELONIDAE																											
Tylosurus cf. *wetzelsdorfensis* (Weinf., 1952)	Pl. 2, Fig. 11		1																								

Table I. Continued.

Taxa		Alpine-Carpathian Foredeep (Molasse)																									
		Moravia																								Lower Austria	Poland
		Localities (number of specimens, this paper)																									
* taxa mentioned in section 4.1	Iconography	1 Borač	2 Boskovice	3 Brno	4 Čebín	5 Cerná Hora	6 Drahanovice	7 Drnovice	8 Hrušovany	9 Kralice n. O.	10 Kurim	11 Lomnice	12 Lomnička	13 Lysice	14 Myslejovic.	15 Nedvědice	16 Přemyslov.	17 Podbřežice	18 Rájec-Jestř.	19 Sudice	20 Šlapanice	21 Voděrady	22 Žabčice	23 Železné	24 Židlochov.		
TRACHICHTHYIDAE																											
Hoplostethus praemediterraneus Schub., 1905	Pl. 5, Fig. 8	227		4				9	2					1							1						
HOLOCENTRIDAE																											
"Myripristis" banatica (Weiler, 1950)	Pl. 5, Fig. 3	1											1														P
ZENIONTIDAE																											
Zenion hololepis (Goode & Bean, 1896)	Pl. 3, Fig. 9	1																									
SCORPAENIDAE																											
Trachyscorpia aff. *cristulata* (G. & B., 1896)	Pl. 5, Fig. 6			1																							
PERISTEDIIDAE																											
Peristedion cf. *cataphractum* (Linnaeus, 1758)	Pl. 3, Fig. 5	1																									
PERCOIDEI incertae sedis																											
"Percoideus" lascivus (Brzobohaty, 1986)	B1986 (Pl. 2, Fig. 3)	1															2										
ACROPOMATIDAE																											
Acropoma nolfi (Steurbaut, 1979)	Pl.3, Fig. 2 5	5										1															
PRIACANTHIDAE																											
Pristigenys rhombica (Schubert, 1906)	Pl. 3, Fig. 6											3															P
APOGONIDAE																											
Apogon imberbis (Linnaeus, 1758)	Pl. 3, Fig. 10	4																									
EPIGONIDAE																											
Epigonus italicus (Bassoli, 1906)	Pl. 3, Fig. 4								1																		
E. remotus (Brzobohaty, 1986)	B1986 (Pl. 1, Fig. 10, 11)	9																									
CARANGIDAE																											
Trachurus sp.	Pl. 3, Fig. 1																1										
HAEMULIDAE																											
Brachydeuterus speronatus (Bassoli, 1906)	Pl. 3, Fig. 3	1						20				1	1												5	LA	P
SPARIDAE																											
Dentex aff. *maroccanus* Valenciennes, 1830	Pl. 5, Fig. 5										1							1								LA	P
Lithognathus aff. *mormyrus* (Linnaeus, 1758)	Pl. 4, Fig. 9	1																									
SCIAENIDAE																											
Argyrosomus regius (Asso, 1801),	Schubert (1906), Opatov																										P
MULLIDAE																											
Mullus sp.	Pl. 3, Fig. 12												1														
CEPOLIDAE																											
Cepola macrophthalma (Linnaeus, 1758)	Pl. 3, Fig. 7			1							1	1														LA	P
Owstonia aff. *neogenica* Nolf & Cappetta 1988	Pl. 3, Fig. 8							1	1								3										

Table I. Continued.

Taxa	Alpine-Carpathian Foredeep (Molasse)																									
	Moravia																									
	Localities (number of specimens, this paper)																									
* taxa mentioned in section 4.1	Iconography	1 Borač	2 Boskovice	3 Brno	4 Čebín	5 Cerná Hora	6 Drahanovice	7 Drnovice	8 Hrušovany	9 Kralice n. O.	10 Kurim	11 Lomnice	12 Lomnička	13 Lysice	14 Myslejovic.	15 Nedvědice	16 Přemyslov.	17 Podbřežice	18 Rájec-Jestř.	19 Sudice	20 Šlapanice	21 Voděrady	22 Žabčice	23 Železné	24 Židlochov.	Lower Austria	Poland
LABRIDAE																										
Thalassoma sp.	Pl. 3, Fig. 11																1										
GOBIIDAE																										LA	
Deltentosteus telleri (Schubert, 1906)	Pl. 4, Fig. 4							4	2	1							1								2		P
Gobius sp.	Pl. 4, Fig. 5	7				1		6		1			7												2		
**Gobiidae* sp. 1	Pl. 4, Fig. 8	5						14				4															
**Gobiidae* sp. 2	Pl. 4, Fig. 7	1						6																			
**Pomatoschistus* ? sp.	Pl. 4, Fig. 3																								2		?
**Istigobius* ? sp.	Pl. 4, Fig. 2	3																					1				
Lesueurigobius vicinalis (Koken, 1891)	Pl. 4, Fig. 1	15						3		1		6					14						1		48		P
**Priolepis* ? sp.	Pl. 4, Fig. 6	3											?1		?1												
SPHYRAENIDAE																										
Sphyraena sp.								1																			
TRICHIURIDAE																										
Aphanopus ? sp.	Pl. 4, Fig. 12	6						4				6															
CAPROIDAE																										
**Antigonia* aff. *capros* Lowe, 1843	Pl. 4, Fig. 13	2						1																	1		LA
Capros ? sp.	Pl. 4, Fig. 10	1																									
SOLEIDAE																										
**Aseraggodes* sp.	Pl. 4, Fig. 11	1																									

Atlantic and West Mediterranean species *T. cristulata* (see Nolf, 2013: pl. 177), but differs from them by the more rounded posterior margin and the perspicuous thickness of the posterior part of the otolith.

Our specimen represents the first otolith-based fossil record of the genus and the whole tribus Sebastolobini (Nolf, 2013). The fish must have measured about 50 cm of TL (compare data by Smale *et al.*, 1995; Quéro *et al.*, 2003).

***Antigonia* aff. *capros* Lowe, 1843** (Pl. 4, Fig. 13a, b). Only subadult otoliths of an *Antigonia* type were found in the Badenian of the Carpathian Foredeep. The largest, from Židlochovice (Pl. 4, Fig. 13), could be fully compared with the holotype of "*Ot. (Monocentridarum) altus*" described by Weiler (1950: pl. 2, fig. 7) from the same stratigraphic level of the Transylvanian Basin and synonymized by Steurbaut (1984) with *A.* aff. *capros*.

Recent *A. capros* lives demersal (with juveniles in the midwater) in the tropical and subtropical waters of the Western and Eastern Atlantic and the Pacific between 50-900 m.

Gobiidae (notice): Gobiid otoliths are very rare in the studied calcareous clays, in comparison with myctophid or macrourid ones, and are represented mainly by juvenile or eroded specimens. There are only two nominally valid species supported by a collection of well-preserved material: *Lesueurigobius vicinalis* (Koken, 1891) and *Deltentosteus telleri* (Schubert, 1906) – see pl. 4, figs 1, 4. Considering the restricted knowledge of Recent gobiid otoliths (Girone *et al.*, 2010) the following taxa are mentioned only at generic level.

***Gobius* sp.** (Pl. 4, Fig. 5a, b). Material: Borač (7 ex.), Černá Hora (1 ex.), Drnovice (6 ex.), Kralice n. O. (1 ex.), Lomnička u T. (7 ex.), Židlochovice (2 ex.). Moderatly elongated, predominant juvenile or corroded gobiid otoliths with outstanding postdorsal and praeventral projection and relatively clear postcaudal iugum. In the Central Paratethys this type of otoliths was usually assigned to the taxon "*Gobius* ex gr. *multipinnatus* (H. v. M.)" (*e.g.*

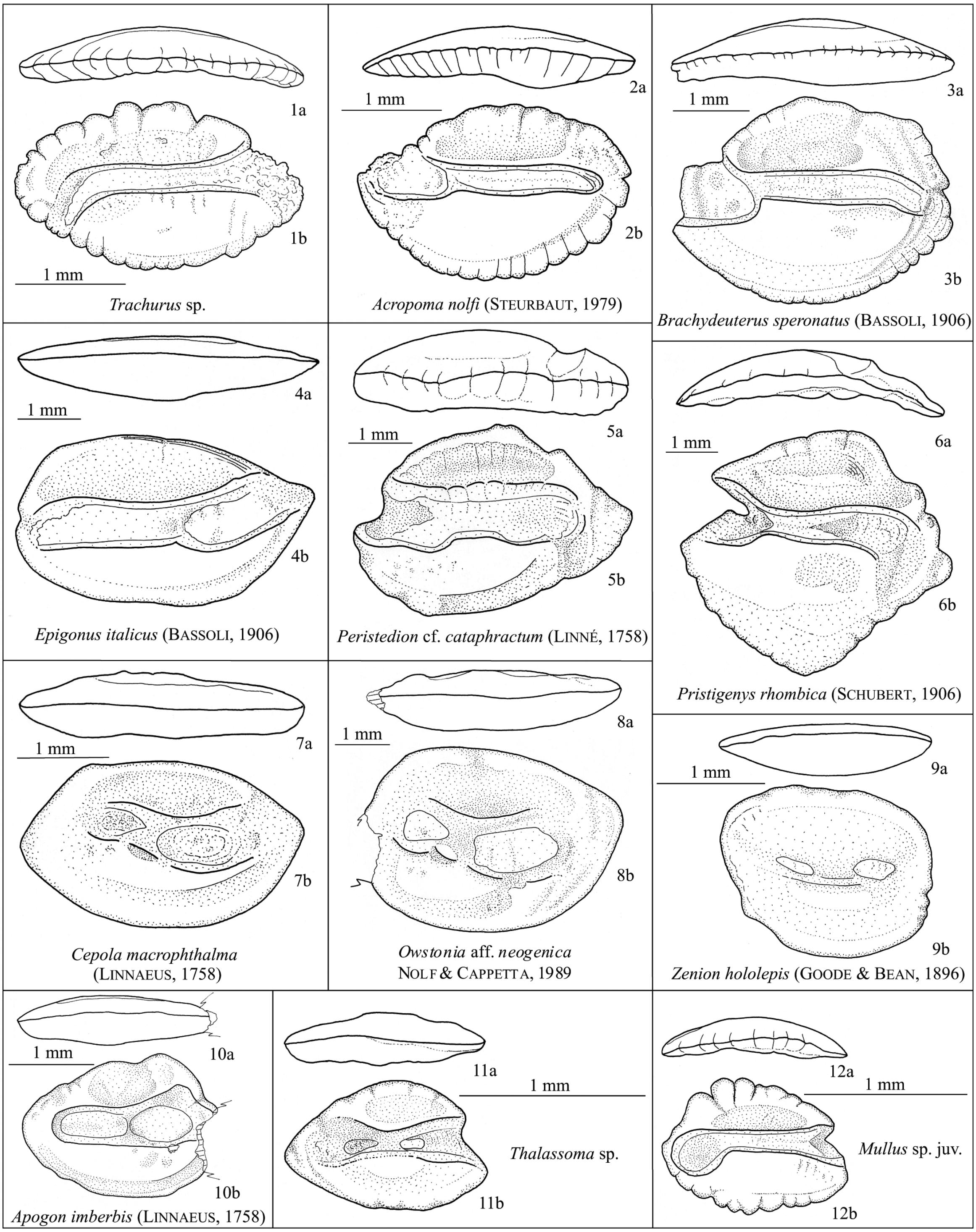

Plate 3. – **1**: *Trachurus* sp.; Židlochovice, Badenian, L (DGS MU Inv. Nr. O 341). **2**: *Acropoma nolfi* (Steurbaut, 1979); Borač, Badenian, R (DGS MU Inv. Nr. O 342). **3**: *Brachydeuterus speronatus* (Bassoli, 1906); Drnovice, Badenian, R (DGS MU Inv. Nr. O 343). **4**: *Epigonus italicus* (Bassoli, 1906); Hrušovany nad Jevišovkou, Badenian, L (DGS MU Inv. Nr. O 344). **5**: *Peristedion* cf. *cataphractum* (Linnaeus, 1758); Borač, Badenian, R (DGS MU Inv. Nr. O 345). **6**: *Pristigenys rhombica* (Schubert, 1906); Lomnice u Tišnova, Badenian, R (DGS MU Inv. Nr. O 346). **7**: *Cepola macrophthalma* (Linnaeus, 1758); Hrušovany nad Jevišovkou, Badenian, L (DGS MU Inv. Nr. O 347). **8**: *Owstonia* aff. *neogenica* Nolf & Capetta, 1989; Přemyslovice, Badenian, L (DGS MU Inv. Nr. O 348). **9**: *Zenion hololepis* (Goode and Bean, 1896); Borač, Badenian, L (DGS MU Inv. Nr. O 349. **10**: *Apogon imberbis* (Linnaeus, 1758); Borač, Badenian, R (DGS MU Inv. Nr. O 350). **11**: *Thalassoma* sp.; Přemyslovice, Badenian, L (DGS MU Inv. Nr. O 351). **12**: *Mullus* sp. juv.; Lomnička, Badenian, L (DGS MU Inv. Nr. O 352).

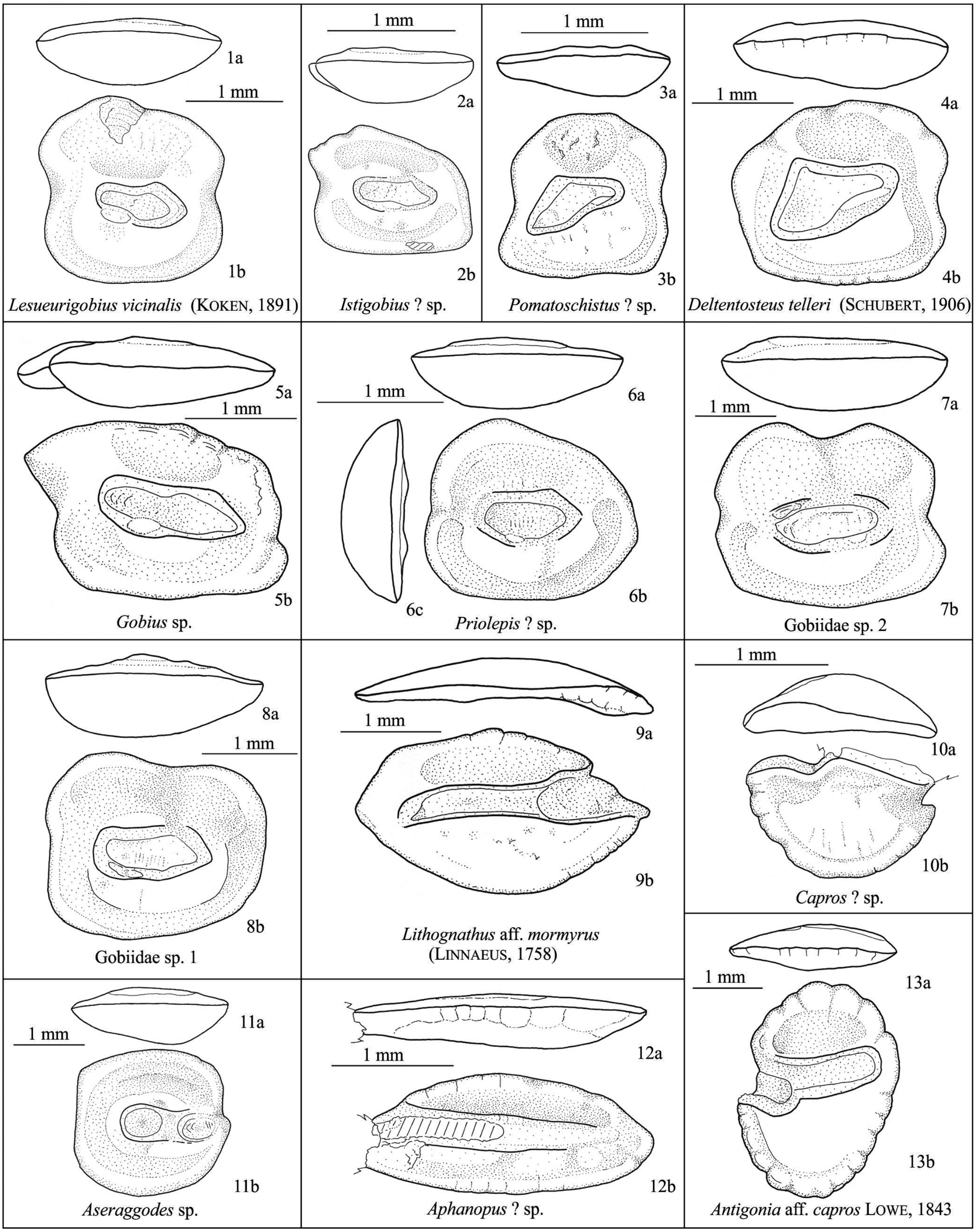

Plate 4. – **1**: *Lesueurigobius vicinalis* (Koken, 1891); Přemyslovice, Badenian, L (DGS MU Inv. Nr. O 354). **2**: *Istigobius* ? sp.; Borač, Badenian, L (DGS MU Inv. Nr. O 355). **3**: *Pomatoschistus* ? sp.; Židlochovice, Badenian, R (DGS MU Inv. Nr. O 356). **4**: *Deltentosteus telleri* (Schubert, 1906); Drnovice, Badenian, R (DGS MU Inv. Nr. O 357). **5**: *Gobius* sp.; Borač, Badenian, L (DGS MU Inv. Nr. O 358). **6**: *Priolepis* ? sp.; Borač, Badenian, L (DGS MU Inv. Nr. O 359). **7**: Gobiidae sp. 2; Drnovice, Badenian, R (DGS MU Inv. Nr. O 360). **8**: Gobiidae sp. 1; Drnovice, Badenian, L (DGS MU Inv. Nr. O 361). **9**: *Lithognathus* aff. *mormyrus* (Linnaeus, 1758); Borač, Badenian, L (DGS MU Inv. Nr. O 362). **10**: *Capros* ? sp.; Borač, Badenian, R (DGS MU Inv. Nr. O 365). **11**: *Aseraggodes* sp.; Borač, Badenian, L (DGS MU Inv. Nr. O 364). **12**: *Aphanopus* ? sp.; Lomnice u Tišnova, Badenian, R (DGS MU Inv. Nr. O 363). **13**: *Antigonia* aff. *capros* Lowe, 1843; Židlochovice, Badenian, L (DGS MU Inv. Nr. O 366).

Brzobohatý *et al*., 2007) whose taxonomical status is based only on the skeletons after the revision published by Gierl and Reichenbacher (2015). Their affinity with the species *G. reichenbacherae* from the Serravallian of the Karaman Basin (Turkey) has also been stated by Schwarzhans (2014). The unsufficient Moravian material does not allow for any more precise systematic conclusions.

Gobiidae sp. 1 (Pl. 4, Fig. 8a, b). Material: Borač (5 ex.), Drnovice (14 ex.), Lomnice u Tišnova (4 ex.). Elongated gobiid otoliths with a perspicuous notch in the dorsal margin seem to be very close to the ones depicted as "genus Gobiidarum" sp. 3 from the Catalunyan Miocene (Hoedemakers and Batllori, 2005: pl. 11, figs 5-8). But the praedorsal part of the Badenian specimens is more developed and their sulcus is clearly located horizontally.

Gobiidae sp. 2. (Pl. 4, Fig. 7a, b). Material: Borač (1 ex.), Drnovice (6 ex.). Well preserved rectangular otoliths (length ~2.5 mm) with rounded postero- and anterodorsal angles, notched middle part of the dorsal margin and a nearly horizontal sulcus. Otoliths with a very similar morphology are figured under different names, e.g., from the Italian Messinian (Girone *et al*., 2010: pl. 10, figs j1a,b, j4, j5). By no means are our otoliths of *Gobius* sp. 2 conspecific with the ones described as *Thorogobius intimus* (Prochazka, 1893) by Schwarzhans (2010: p. 265, pl. 106, figs 11-13) from the Badenian of Slovakia and Austria, which have an oblique anterodorsal margin.

***Pomatoschistus* ? sp**. (Pl. 4, Fig. 3a, b). Material: Židlochovice – two well preserved and (?) juvenile specimens. These otoliths seem to be conspecific with those described by Radwanska (1992: p. 292, pl. 35, figs 3-4, tex-fig. 150a-d) as "*Ot. Gobiidarum* sp. 5" from the Badenian of Korytnica.

***Istigobius* ? sp.** (Pl. 4, Fig. 2a, b). Material: Borač (three specimens), Žabčice (1 ex.). One figured otolith is well preserved and comparable with the otoliths of the present day species *I. decoratus* (Herre, 1927) and *I. ornatus* (Rüppel, 1830) – see Smale *et al*., 1995: pl. 129, figs C and D, respectively, and Rivaton and Bourret, 1999: pl. 79, figs 9-10. Both species are widespread in the Indo-Pacific waters including the Red Sea and the presence of this genus in the Middle Badenian Sea can be considered as probable. Otoliths described as "*genus Gobiidarum*" sp. 2 from the Burdigalian/Langhian of the Catalunya (Hoedemakers and Batllori, 2005: pl. 12, figs 3-7) also show a very similar morphology.

***Priolepis* ? sp.** (Pl. 4, Fig. 6a, b, c). Three gobiid otoliths from Borač show the following characters: a prominent anterior margin; a nearly vertical posterior margin with a small notch in its center; a horizontal sulcus; a flat ventral field with a ventral ridge and a deep and wide depression in the dorsal area. These characters, together with the ventral and posterior views, are quite similar to what is seen in otoliths of the West Atlantic *P. hippoliti* (Metzelaar, 1922) (see Nolf and Brzobohatý, 2009: pl. 8, fig. 4) and of *P. cincta* (Regan, 1908) (see Smale *et al*., 1995: pl. 129 H) from the Indo-Pacific realm, including the Red Sea. The otoliths figured by Brzobohatý *et al*. (2007: pl. 8, figs 9-11) under the name *Priolepis* sp. from the Badenian of the Vienna Basin belong to another genus (see Nolf and Brzobohatý, 2009: p. 329).

***Aseraggodes* sp.** (Pl. 4, Fig. 11a, b). A slightly eroded flatfish otolith from Borač has a sulcus, with more or less circular colliculi and shows some similarity with otoliths of the present day *A. cyaneus* (Alckock, 1890) (see Schwarzhans, 1999: figs 859-861) and may belong to the same genus. There is only one other fossil species of *Aseraggodes*: *A. laganus* Girone & Nolf, 2009 from the North Italian Upper Eocene, which is characterised by a clearly longer ostium. The genus *Aseraggodes* does not live in the present day Mediterranean, but many Recent species are widely distributed throughout the Indo West Pacific.

Description of new species

Order ATELEOPODIFORMES Berg, 1937
Family ATELEOPODIDAE Kaup, 1858
Genus *Ijimaia* Sauter, 1905
***Ijimaia rara* n. sp.**
Pl. 5, Fig. 7a, b

Ijimaja sp. – Nolf, 2013: p. 48, pl. 53

Derivatio nominis: *rarus, a, um* = scarce, refers to the solitary occurrence of the holotype.

Holotype: a left otolith (Pl. 5, Fig. 7), deposited in the collections of the Masaryk University (DGS MU Inv. Nr. O 373).

Stratum typicum: calcareous clay of the Badenian (= Langhian, Middle Miocene) at Borač (Carpathian Foredeep, Middle Moravia, Czech Republic).

Dimensions: L = 10.9 mm; H = 8.4 mm; T = 2.9 mm; OL:OH = 1.3

Diagnosis

This species is characterized by thick, sub rhomboidal otoliths showing a nearly rectangular ventral half with a smooth surface. The dorsal half shows a strong posterior expansion, and the whole upper rim is lobated. The lobes are separated by well-incised radial furrows that continue downwards to near the crista superior. The sulcus is not divided in an ostial and a caudal portion and both the crista superior and the crista inferior are very salient, resulting in a sulcus, that is somewhat extruding from the inner face. The crista inferior has a spine-like anterior expansion.

Affinities

Our specimen is quite similar to otoliths of the Recent eastern Atlantic species *Ijimaia loppei* Roule, 1922 (see Nolf,

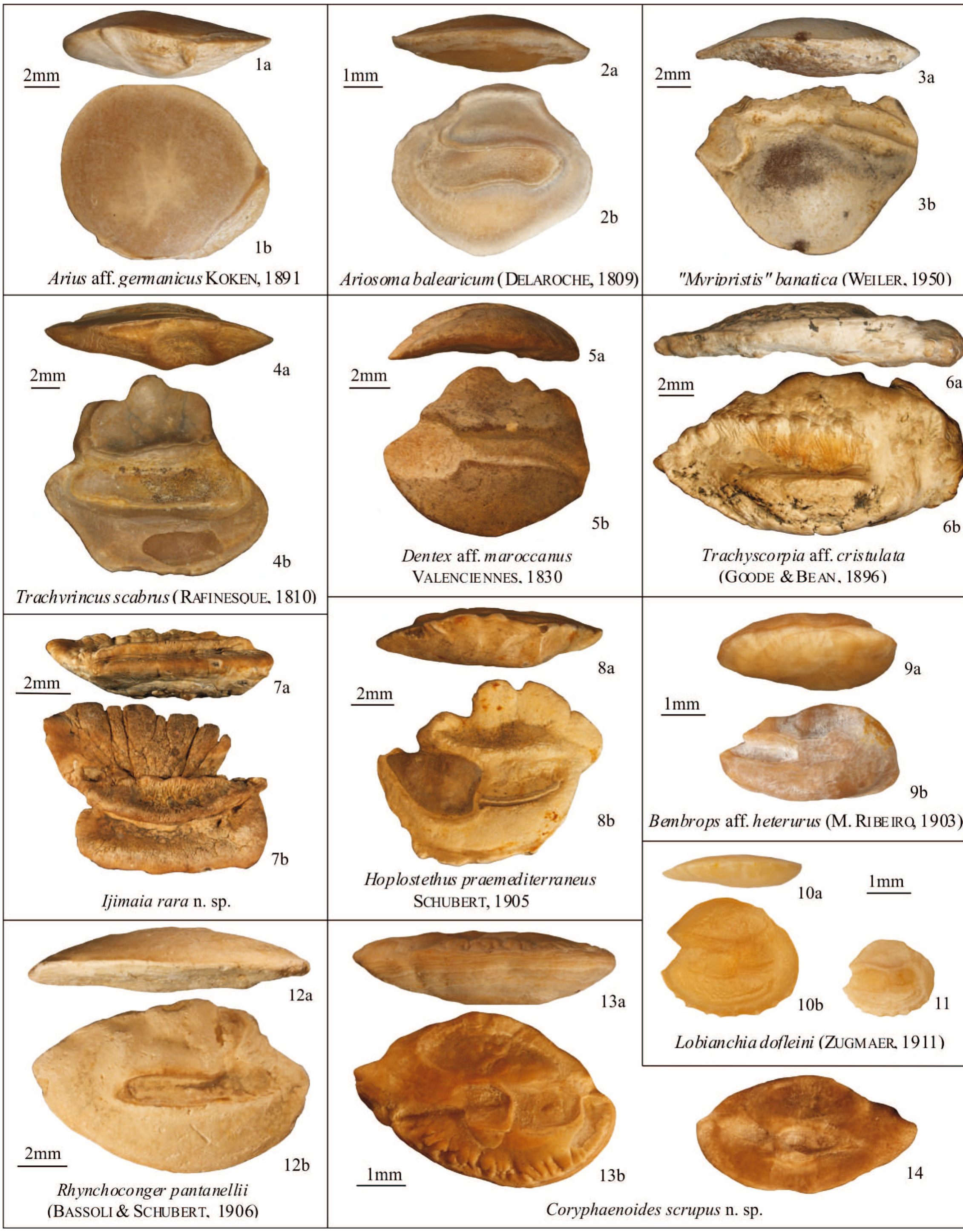

Plate 5. –**1**: *Arius* aff. *germanicus* Koken, 1891; Lomnice u Tišnova, Badenian (DGS MU Inv. Nr. O 367). **2**: *Ariosoma balearicum* (Delaroche, 1809); Brno-Královo Pole, Badenian (DGS MU Inv. Nr. O 368). **3**: "*Myripristis*" *banatica* (Weiler, 1950); Borač, Badenian (DGS MU Inv. Nr. O 369) **4**: *Trachyrincus scabrus* (Rafinesque, 1810); Brno-Královo Pole, Badenian (DGS MU Inv. Nr. O 370). **5**: *Dentex* aff. *maroccanus* Valenciennes, 1830; Podbřežice, Badenian (DGS MU Inv. Nr. O 371). **6**: *Trachyscorpia* aff. *cristulata* (Goode and Bean, 1896); Brno-Královo Pole, Badenian, (DGS MU Inv. Nr. O 372). **7**: *Ijimaia rara* n. sp.; Borač, Badenian, holotype (DGS MU Inv. Nr. O 373). **8**: *Hoplostethus praemediterraneus* Schubert, 1905; Borač, Badenian (DGS MU Inv. Nr. O 374). **9**: *Bembrops* aff. *heterurus* (M. Ribeiro, 1903); Mühlbach a. M., Austria, Badenian, Depo: B. Reichenbacher, Munich. **10, 11**: *Lobianchia dofleini* (Zugmayer, 1911); Mühlbach a. M., Austria, Badenian, Depo: B. Reichenbacher, Munich. **12**: *Rhynchoconger pantanellii* (Bassoli and Schubert, 1906); Borač, Badenian (DGS MU Inv. Nr. O 375). **13, 14**: *Coryphaenoides scrupus* n. sp.; Lysice, Badenian (DGS MU Inv. Nr. O 376 = holotype, Inv. Nr. O 377 = paratype).

2013, pl. 53). It clearly differs from the Recent species by the rhomboidal outline, the shorter anteroventral portion, the well marked posterodorsal expansion and the clearly convex outer face. Otoliths of the present day species – *I. antillarum* Howell Rivero, 1935 from the W Atlantic; *I. dofleini* Sauter, 1905 from the NW Pacific; *I. plicatellus* (Gilbert, 1905) from the Pacific – are more different. Otoliths from the NW Pacific taxa *I. fowleri* Howell Rivero, 1935 remain unknown.

Remark

Ateleopodids are exclusively marine fishes with a poor fossil record. Scarce otoliths of *Ateleopus* (*A. ariejansseni* Schwarzhans, 2010 and *A. nolfi* Schwarzhans, 2010) are known from the earliest Middle Miocene of the North Sea Basin only (Huyghebaert and Nolf, 1979; Schwarzhans, 2010). The Badenian occurrence is the first otolith-based fossil record of the genus *Ijimaia*. Thus, the Middle Miocene occurrence of otoliths of *Ijimaia* and *Ateleopus* indicates a taxonomic diversification of the ateleopodids at least before the Middle Miocene, which is in accordance with the Actinopterygian time-calibrated phylogeny interpreted by Near *et al*. (2012: figs 1, S1). *Ijimaia* species are demersal and bathydemersal fishes, usually living in depths of under 200 m. Our specimen from Borač could represent a large jellynose fish, *e.g. I. loppei* from near Gibraltar and the Celtic Plateau area can grow up to 2 m (Quéro *et al*., 2003).

Order GADIFORMES Goodrich, 1909
Family MACROURIDAE Bonaparte, 1832
Genus *Coryphaenoides* Gunner, 1765
***Coryphaenoides scrupus* n. sp.**
Pl. 5, Figs 13a, b, 14

Derivatio nominis: scrupus (Latin) = pointed stone; refers to the posterior end of the otoliths.

Type material: holotype: a left otolith (Pl. 5, Fig. 13), deposited in the collection of the Masaryk University, Brno (DGS MU Inv. Nr. O 376); two paratypes, of which one is figured (Pl. 5, Fig. 14) and one is badly eroded (DGS MU Inv. Nr. O 377, 378).

Stratum typicum: Calcareous clay of the Badenian (= Langhian, Middle Miocene) at Lysice (Carpathian Foredeep, Middle Moravia, Czech Republic).

Dimensions: L = 5.6 mm; H = 3.6 mm; L:H = 1.6 (Pl. 5, Fig. 13, Holotype); 5.2 mm; 2.9 mm; 1.8 (Pl. 5, Fig. 14, Paratype).

Diagnosis

This species is characterized by thick, moderately compressed otoliths, OL:OH = 1.6-1.8. The dorsal part is convex, and more expanded postdorsally. The ventral portion is most developed in its anterior portion and becomes more slender towards the posterior end of the otolith. The ventral rim is finely crenulated. The posterior end is pointed and sharp, especially in the holotype. The anterior rim shows a very slight excisura. The collum is much higher than wide, without collicular crest. Both collicula are distinct and well separated, deep and of similar proportion. There is a deep and wide dorsal depression just above the crista superior. The ventral area bears a furrow distinctly close to the anterior part of the otolith. The outer face is regularly convex with several radial furrows near the ventral rim.

Discussion

In the fossil record, otoliths of seven extinct species of *Coryphaenoides* are known from Oligocene to Pliocene deposits of the Mediterranean and Paratethys regions. In the latter region, three previously described Badenian species are contemporaneous with the new taxon: *C. hansfuchsi* (Schubert, 1905), *C. gaemersi* (Brzobohatý, 1986) and *C. kalvodai* Brzobohatý, 1995. Otoliths of *C. scrupus* resemble, to a certain extent, those of *C. gaemersi* only, but they differ from them by their very narrow collum, their sharp posterior tip, their convex dorsal rim, and the deeper and wider depression in their dorsal area. There are about sixty-five Recent species of *Coryphaenoides*. Eleven of them live in the eastern Atlantic – with two West Mediterranean invaders – *C. guentheri* (Vaillant, 1888) and *C. mediterraneus* (Giglioli, 1893), and their otoliths are well known (see Nolf, 2013: pls 91, 92 and IRSNB collections). Otoliths of *C. scrupus* show some similarity with those of *C. guentheri* only, but differ mainly in the somewhat less compressed outline (L:H < 1.6; Campana, 2004: p. 61; Swan and Gordon, 2001: fig. 3b), more elliptical collicula, and a blunt posterior end. The same could be stated for otoliths described as *C.* cf. *guentheri* from the South Italian Pleistocene (Girone, 2003: pl. 1, fig. 6a, b, c).

DISCUSSION

Carpathian Foredeep in Moravia

More than 36,000 otoliths of bony fishes from more than 24 surface exposures (Tab. Ia-e) and three boreholes (Rybníček HV-5, Brzobohatý, 1981; Židlochovice – 1 and 2, Doláková *et al*., 2014; Lomnička-1, Holcová *et al*., 2016) were obtained from clays of the Badenian Carpathian Foredeep in southern Moravia. They allowed the identification of a fish fauna of 84 nominal species and 22 taxa in open nomenclature (Tab. Ia-e).

Among the 84 nominal species, 27 are still represented in the Recent fauna; the following are common in the Mediterranean region and widespread in the Adriatic: *Apogon imberbis, Argyrosomus regius, Ariosoma balearicum, Cepola macrophthalma, Coelorinchus caelorhinchus, Conger conger, Dentex maroccanus, Gadiculus argenteus, Glossanodon* *leioglossus, Hygophum hygomii, Lithognathus mormyrus, Maurolicus muelleri, Merluccius merluccius, Peristedion cataphractum, Trachyrincus scabrus* and *Vinciguerria poweriae*.

Nezumia aequalis and *Valenciennellus tripunctulatus* are oceanic species found in the Western Mediterranean; *Antigonia capros, Scopelarchus guentheri, Xenodermichthys copei* and *Zenion hololepis* represent cosmopolitan oceanic species that are also widespread outside the Mediterranean. *Bonapartia pedaliota* nowadays lives in the Eastern Atlantic and Indian Ocean, *Diaphus taaningi* in the Atlantic and Western Pacific; *D. regani* is Indo-West-pacific. *Trachyscorpia cristulata* is also a typical representative of the Atlantic Ocean fauna. *Physiculus huloti* is nowadays widespread in the eastern Atlantic, from Angola to Mauritania.

In addition to myctophids, *Vinciguerria poweriae* (8 locations; 143 individuals from Borač) and *Gadiculus argenteus* (17 locations; 485 individuals from Drnovice) represent the highest frequency of Recent species in the studied sites.

Myctophids (91% of the otolith assemblage, 16 nominal species), followed by Stomiiformes (3% of all otoliths, 6 nominal species) and macrourids (1.6% of all otoliths, 13 nominal species) dominate the Badenian otolith based fish fauna. This substantial part of the community is further complemented by Bregmacerotidae, Gadidae and Trachichthyidae represented each by only a single, but individually numerous species.

The mesopelagic myctophids are a dominant part of the association at all studied sites of the Carpathian Foredeep. Their otoliths are, however, often eroded, or represented by juvenile individuals. Sixteen (16) valid species are recorded from the Badenian Carpathian Foredeep in Moravia. Among them, *Diaphus regani, D. taaningi*, and *Hygophum hygomii* are still living in Recent seas. *Diaphus cahuzaci* and *D. debilis* are common species in 20 localities. The widespread species include *D. acutirostrum* (17 locations), *D. kokeni* (16 localities) and *D. haereticus* (15 sites). This assemblage is significantly complemented by other *Diaphus* species, by *Benthosema fitchi* (relatively numerous in 11 localities), *Notoscopelus mediterraneus* (14 sites) and *Lampichthys schwarzhansi* (10 localities). Representatives of species of *Hygophum, Lampadena* and *Symbolophorus* are rather rare.

Numerically, the diversity of the Badenian myctophids in the Carpatian Foredeep (16 species, 7 genera) corresponds very well with the current situation in the Mediterranean (17 species, 11 genera), but the diversity in species of the genus *Diaphus* in the Badenian is twice as high as in the Recent communities of the Mediterranean (8 species versus 4), and the genera *Lampadena* and *Lampichthys* are missing in today's Mediterranean (Froese and Pauly, 2016). The presence of otoliths of *Lampichthys* in the Badenian deposits seems exotic. In the Recent fauna, there is only a single species, *Lampichthys procerus* (Brauer, 1904), with a circum-global distribution in the subtropical southern hemisphere (Froese and Pauly, 2016). A second fossil species, *Lampichthys mangapariensis* Schwarzhans, 1980, is also tied to the southern hemisphere (New Zealand, Upper Miocene). *Lampichthys schwarzhansi* obviously represents a remainder of the Paleotethys fish fauna that is only documented from the Central Paratethys (Carpathian Foredeep in Moravia and Poland, and in the Vienna Basin).

In the Recent mesopelagic fauna, myctophids represent the largest group of mesopelagic fishes and are distributed in all oceans. They are diurnal fishes, most abundant at depths of 200-1000 m during daytime, emerging to almost the surface at night (Froese and Pauly, 2016). For some deeper water taxa, like *Lampadena* and *Notoscopelus,* adults migrate vertically in a very limited scope, possibly not at all (Nafpaktitis *et al*., 1977).

Macrourids are also highly diversified: 14 species (7 genera) of which three Recent ones are represented. The most frequent one, *Gadomus tejkali*, was found at 15 sites. *Coelorinchus macruruloides* and *Nezumia aequalis* are also quite regularly represented. For *Trachyrincus scabrus,* important numbers of mature individuals are found at one location (Brno-Královo Pole) only. Unlike for myctophids, the diversity of macrourids in the Badenian of the Carpathian Foredeep is significantly higher than in the present day Mediterranean (7 species / 5 genera) (Froese and Pauly, 2016) and is very close to the diversity of the group in the Tortonian of the Mediterranean (12 species / 7 genera; Lin *et al*., 2017). Today, the genera *Coelorhinchus*, *Coryphaenoides*, *Nezumia,* and *Trachyrincus* are still living in the Mediterranean (Froese and Pauly, 2016), while *Bathygadus, Gadomus, Macrouroides,* and *Sphagemacrurus* are absent. Badenian macrourids are represented by two bathymetrically distinct groups: Recent *Bathygadus, Nezumia* and *Coelorinchus* rise up to the lower limit of the continental platform, the latter genus sometimes up to the 90-meter border (Froese and Pauly, 2016). They represent, in a sense, "the shallow water group". The deeper living group includes *Gadomus, Macrouroides* and *Trachyrincus*, which do not rise higher than 400 m, and *Coryphaenoides*, which lives in depths over 300 m (Froese and Pauly, 2016). Macrourids are specialized, primarily benthopelagic fishes, inhabiting continental slopes with sharply defined areas, and with a tendency to endemism (Cohen *et al*., 1990).

Stomiiforms (Gonostomatidae, Sternoptychidae, Phosichthyidae and Stomiidae) display a significant diversity in the Badenian of the Carpathian Foredeep (11 taxa). This agrees well with the presence of many other groups of deep-water fishes and also corresponds with the diversity of stomiiforms in the Recent Mediterranean (12 taxa, however with a clearly different generic composition (Froese and Pauly, 2016)). This is higher than the diversity of the group in the North Italian Tortonian (Lin *et al*., 2017), where phosichthyids are represented by rather numerous specimens of the genus *Vinciguerria*. In the Carpathian Foredeep, *Vinciguerria poweriae, Maurolicus muelleri* and *Valenciennellus tripunctulatus* are dominant in numbers of specimens. Other taxa are represented mainly by smaller numbers of individuals and in more scattered localities. Recent species of *Phosichthys* are distributed in southern seas, while *Woodsia* is also reported from the region of Bermuda (Froese and Pauly, 2016). Their presence in the Badenian of the Central Paratethys indicates the existence of Tethys communities of the paleomediterranean fauna in this area that were later reduced or eliminated by Messinian and Pliocene changes (Brzobohatý and Nolf, 2002).

A distinctive feature of the Badenian foredeep area (2.5% of all otoliths) is also the presence of *Gadiculus argenteus* in 17 locations, sometimes in significant amounts (485 individuals in Drnovice). Other gadids documented further north from the same stratigraphic level in Poland (*Trisopterus, Micromesistius*) (Radwanska, 1992) are absent in the southern Moravian foredeep. In the borehole profile Lo-1 *G. argenteus* is represented by increased numbers above the LO level of *Helicosphaera waltrans*. This may be associated with colder oscillations in the early Middle Miocene Climatic Transition (Holcová *et al*., 2016).

Otoliths of *Bregmaceros albyi* are relatively numerous, primarily at Borač, while at the other five locations they occur only sporadically. These are epipelagic fishes whose osteology, including *in situ* otoliths, and relationships within the history of the entire genus were discussed in detail in Přikryl *et al*. (2016).

In the trachichthyids, otoliths of *Hoplostethus praemediterraneus* are very numerous near Borač, while at the five other localities, they occur only sporadically. In the Recent Mediterranean, *H. mediterraneus* Cuvier, 1829, a cosmopolitan benthopelagic species with a considerable bathymetric range (100 to 1200 m) is the only representative of the genus (Froese and Pauly, 2016).

Ophidiids are significantly represented only by *Glyptophidium major* at 6 localities, but only in Borač and Drnovice their number exceeds 10 specimens. Today, the genus is represented mainly by bathydemersal fishes on the outer shelf and upper slope of the Indian-Pacific area (Froese and Pauly, 2016).

Besides the abovementioned groups with frequent species and otoliths there are 32 taxa that occur at one site only and are represented by a few otoliths only. They include 21 nominal species and 11 taxa, which could only be identified in open nomenclature.

The majority of the documented genera (55) still lives in the Mediterranean today. The remaining genera (35) can be considered as being part of a paleomediterranean ichthyofauna that is nowadays absent there, but can be found in the adjacent parts of other oceans:

– *Aphanopus, Bathygadus, Brachydeuterus, Gadomus, Ijimaia, Physiculus, Polyipnus* and *Pterothrissus* in the Eastern Atlantic (up to Gibraltar),

– *Acropoma, Aseraggodes, Atherinomorus, Bathycongrus, Etrumeus, Glyptophidium, Hoplobrotula, Istigobius, Owstonia, Priolepis, Pristigenys* and *Sphagemacrurus* in the western Indian Ocean (including the Red Sea) and potentially also in the Pacific Ocean,

– *Antigonia, Arius, Bonapartia, Bregmaceros, Hemiramphus, Lampadena, Macrouroides, Melanonus, Sagamichthys, Scopelarchus, Xenodermichthys, Zenion* and perhaps also *Woodsia* in both aforementioned regions.

– *Lampichthys* and *Phosichthys* are nowadays typical representatives of southern seas (Quéro *et al*., 2003; Froese and Pauly, 2016). The above-mentioned otolith assemblage was evaluated in the past for paleobathymetry (Nolf and Brzobohatý, 1994a) and used for the interpretation of depth ratios of the Badenian Sea of the Carpathian Foredeep in Moravia (Brzobohatý, 1997, 2001; Doláková *et al*., 2008), but also for the bathymetric interpretation of the junction of the Vienna Basin with the Carpathian Foredeep in this time interval (Brzobohatý and Stráník, 2012). The Badenian sedimentation area in the Moravian foredeep is considered as a peripheral basin of the Carpathian orogenic belt where a very rugged older relief of the western edge of the Bohemian Massif was completely flooded (*e.g*. Kováč *et al*., 2007). The interpreted isobath lines document more than 400 m water depth in the immediate foreground of the flysch nappes of the Western Carpathians as well as the general shallowing of the basin to the west into the Bohemian Massif (Brzobohatý, 1997).

In the southernmost Moravia a homogenous deep-water otolith association suggests connection with nearly identical communities in the NW tip of the Vienna Basin. This similarity documents a relatively deep linking (> 200 m) of both basins across the area of flysch nappes around Mikulov (Fig. 1c). The establishment of this connection is related to recurrent movements along old faults with NW-SE direction in the Dyje (Thaya) depression and with a significant decrease of block flysch in the Waschberg Zone (Brzobohatý & Stráník, 2012).

In the westernmost part of the Carpathian Foredeep (*e.g*. Kralice and Oslavou, Czech Moravian Highlands, Fig. 1c) the otolith fauna from the Badenian denudation relics indicates shallower sedimentation conditions. Even shallower conditions (< 100 m) are documented by otoliths in the northernmost part of the Boskovice Furrow around Lanskroun.

Here, we can also find taxa, which tolerate a reduced salinity: the sciaenid *Argyrosomus regius* near Opatov and more numerous gobiids (Procházka, 1900; Schubert, 1906).

The paleobathymetrics mentioned above (see individual sites in Brzobohatý, 1997) can be accepted even after a

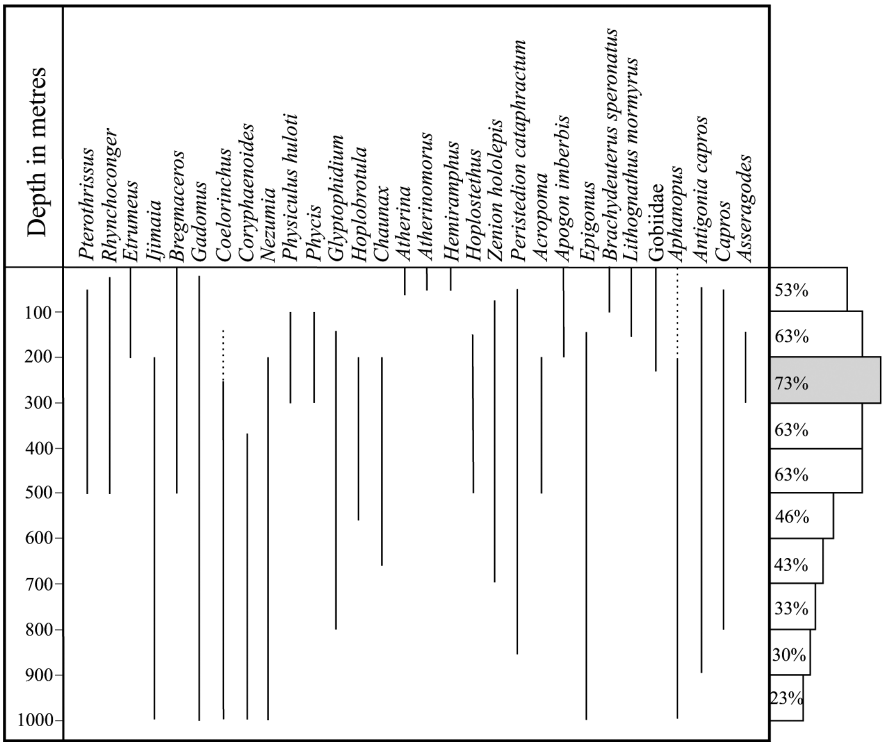

Figure 3. – Present-day bathymetric range of benthic and benthopelagic taxa (without pelagic taxa) (Jardas, 1996; Quéro *et al.*, 2003; Froese and Pauly, 2016) represented in the Badenian clay of the Borač Section (compare Brzobohatý, 1997).

methodical refinement based on actuo-paleontological studies in recent NE Atlantic sea bottoms (Lin *et al.*, 2016), that draw attention to the role played by mesopelagic elements at depths shallower that 500 m, which results in a shifting of subsequent calculations towards greater depths. A paleobathymetric chart of the Borač section (Tab Ia-c, Locality No. 1) excluding mesopelagic species shows depths of 200-300 m (Fig. 3) and can serve as an example, when compared to the same chart including mesopelagic elements (Brzobohatý, 1997: fig. 5). The same could be stated in the case of the deepest locality Brno-Královo Pole (Tab. Ia-c, Locality Nr. 2). Paleobathymetric chart including all teleost taxa shows depths of 400-700 m (Brzobohaty, 2001: fig. 4, Brno-Královo Pole) and 400-600 m in the case of new data excluding mesopelagic species (Fig. 4). Deep environment of the locality could be supported by unusual high number of *Trachyrincus scabrus* otoliths (134, see Tab. Ic). Otolith paleobathymetry on some other localities (Lomnička, Tab 1a-c, Locality Nr. 12; Židlochovice, Tab. 1-c, Locality Nr. 24) corresponds also very well with general sedimentological, gamma-spectrometric, foraminiferal, calacreous nannoplankton, and otolith data published in new summary papers on Badenian in the Carpathian Foredeep (Doláková *et al.*, 2014; Holcová *et al.,* 2016).

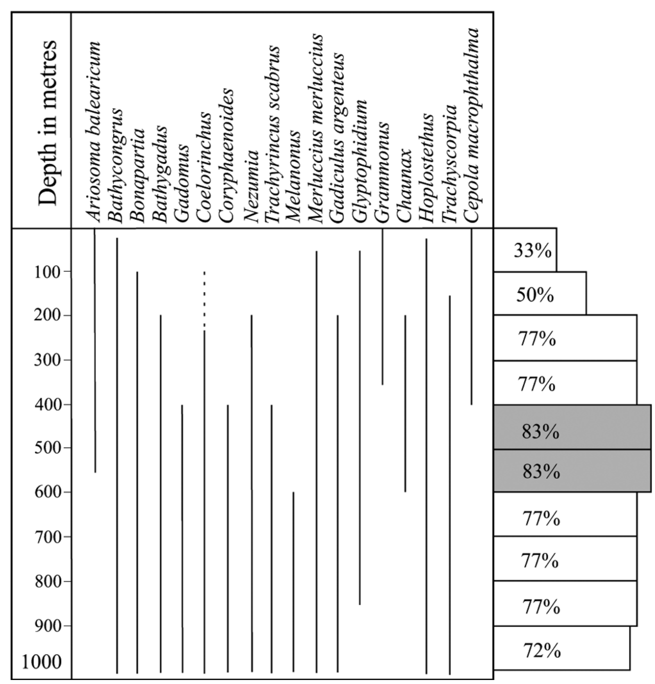

Figure 4. –Present-day bathymetric range of benthic and benthopelagic taxa (without pelagic taxa) (Jardas, 1996; Quéro *et al.*, 2003; Froese and Pauly, 2016) represented in the Badenian clay of the Brno-Královo Pole section (compare Brzobohatý, 1997).

The same otolith association, as discovered in surface outcrops within the studied stratigraphic level, was not detected in NE Moravia and Silesia. Impoverished early Badenian otolith communities, with *Diaphus debilis,* juvenile *Diaphus, Maurolicus muelleri, Valenciennellus tripunctulatus* and fragments of gadids (Cicha *et al.*, 1985), were documented in boreholes OS-1 Kravaře and OS-2 Hať only

(Fig. 1a), indicating the continuity of an otolith association of deep-water type towards the Polish foredeep (see below).

The Molasse of Lower Austria

Twenty-five taxa are known from the Lower Austrian Molasse (Grund Fm., Gaindorf Fm. – Fig. 1; Schubert, 1906; Weinfurter, 1952; Schultz, 2013; newly collected material from the Mühlbach am Mannhartsberg site – see Tab. Ia-e, Lower Austria column). Among them, there are 19 nominal species, of which 16 are also known from the Badenian of the Carpathian Foredeep in Moravia. Three Lower Austrian species represented by a few otoliths (*Lobianchia dofleini, Bembrops* aff. *heterurus* – see Pl. 5, Figs 9 and 10, 11 and "*Sparus" noetlingi* – see Schubert, 1906: pl. 18, fig. 14) have not been found in Moravia. Five more taxa are represented by badly preserved otoliths, allowing assignment in open nomenclature only: *Gnathophis* sp., *Owstonia* sp., ?*Pomadasys* sp., *Dentex* sp., Sciaenidae ind. There are, however, numerous otoliths of neritic gobiids that are currently being studied by Bettina Reichenbacher (oral communication). Otoliths of the pelagic *Gadiculus argenteus* are relatively common.

The otolith association of the Lower Austrian Molasse (despite the lower number of sites and the lower number of species) qualitatively differs from the fauna of the depression areas of the foredeep in Moravia by the complete absence of stomiiforms and deep-water macrourids (with the exception of juvenile specimens of *Gadomus tejkali*). Moreover, the diversity of mesopelagic myctophids is clearly lower (absent are *Hygophum, Lampadena, Notoscopelus, Symbolophorus* and *Myctophum*) and the presence of neritic gobiids is significantly higher. This is in accordance with the paleobathymetry of the Gaindorf Formation near Mühlbach am Mannhartsberg (deep neritic / upper bathyal; Rögl and Spezaferri, 2003), calculated on the basis of Foraminifera, and ultimately also on fish teeth (neritic; Schultz, 2003).

The Carpathian Foredeep in Poland

The otoliths of the early Badenian Carpathian Foredeep in Poland were first studied by Chaine and Duvergier (1928), later by Smigielska (1966, 1973, 1979) and Radwanska (1992); some are also mentioned in Schwarzhans (2010). There are relatively few species in common with the foredeep in Moravia (~33, *i.e.* approx. 30%, see Tab. I), because ecologically different communities are involved. Gobiid otoliths (at Korytnica, Weglinek) and gadids (at Nawodzice, Rybnica) predominate especially here, accompanied mostly by other shallow-water groups. The aforementioned sites are located in the peripheral part of the foredeep relatively far from the edge of the flysh nappes (Fig. 1a). Only in the westernmost section near Beczyn (near Wadowice), situated in the immediate foreground of the nappes, there is a significant increase in the proportion of myctophids.

This obvious disparity in the otolith associations from the same stratigraphic level in Moravia and Poland is in accordance with the geotectonic locations of the studied profiles. Badenian sediments in South Moravia are remnants of deeper facies of the basin in the immediate foreground of pre-Badenian nappes (*e.g.* Brzobohatý, 1997) and their distal shallow water equivalents are significantly denudated towards the west into the Bohemian Massif. The inner proximal facies of the early Badenian in Poland are thrusted by younger styrian nappes (Oszczypko and Oszczypko-Clowes, 2012) and ahead of their forefronts only outer shallow-water facies are preserved.

Especially in the Polish Korytnica Basin, these facies show a significantly higher frequency of fishes favouring colder water (*Gadiculus*, *Merluccius*, *Phycis*, *Ciliata, Gaidropsarus, Micromestistius* and *Trisopterus*) compared to the Moravian foredeep, where only the first three of these genera are known. This supports the interpretation of a north-south temperature gradient in the Central Paratethys region in this period (Harzhauser *et al*., 2003; Brzobohatý *et al*., 2007).

SUMMARY AND CONCLUSIONS

– The Badenian otolith assemblage of the Carpathian Foredeep in Moravia contains 84 nominal species of which *Ijimaia rara* and *Coryphaenoides scrupus* are new. This assemblage, combined with those of the Lower Austrian and Polish Foredeep, provides a very well documented fauna (~150 nominal species), which is quantitatively comparable to, *e.g.* the ones of the Oxlundian and Reinbekian in the North Sea Basin (Schwarzhans, 2010) and of the Langhian in the Aquitaine Basin (Nolf and Brzobohatý, 2002).

– The myctophids (91% of the otolith assemblage, 16 nominal species) dominate quantitatively, complemented by stomiiformes (3% of the assemblage, 6 nominal species) and macrourids (1.6% of the assemblage, 13 nominal species). This substantial part of the composition is complemented by Bregmacerotidae, Gadidae and Trachichthyinae, which are represented each by a single species that occurs in relatively important numbers.

– *Trachyscorpia* cf. *cristulata* represents the first otolith based fossil record of this still living species and of the entire tribe Sebastolobini. Otoliths of *Serrivomer* and *Ijimaia* (already mentioned in Nolf, 2013) represent the first fossil records for these genera. The first record of platytroctids (*Sagamichthys*?) is also highly probable. Species of *Nansenia* and *Zenion* represent the first Paratethys record.

– The otolith association shows paleobathymetric ratios, reaching a depth of more than 400 m in the South Moravian depressions of the foredeep basin, and demonstrates the deep neritic nature of its links to the Vienna Basin in the South and to the Polish parts of the foredeep basin in the North.

The appearance of numerous otoliths of *Gadiculus argenteus* indicates the onset of cold oscillations, associated with the onset of the Middle Miocene Climatic Transition.

– The differences in the composition of the otolith associations between the Badenian foredeep in Moravia and Poland can be attributed to:

1) primarily, the first signs of climatic zonation during the Middle Badenian (in the sense of Hohenegger *et al*., 2014) and documented by a higher proportion of gadids in Poland;

2) secondary, by the geotectonic situation of the Badenian foredeep in the foreground of nappes, in which the sediments in southern Moravia remained in their original position but were eroded in the western periphery of the basin, due to extensive denudation. In northern Moravia and Silesia and in Poland the proximal and central foredeep sediments were covered by younger styrian nappes, and only outer shallow-water developments remained ahead of their forefronts. It is, however, also possible that the foredeep developments in Poland were shallower than in South Moravia.

– The Badenian otolith associations of the Austrian Molasse, of the Carpathian Foredeep in Moravia and in Poland represent a substantial part of species described in this stratigraphic interval for the entire Central Paratethys.

– The Badenian otolith association of the Central Paratethys shares 55 (~46%) species with the Tortonian fauna of the Mediterranean (Lin *et al*., 2017), of which 24 are Recent. This documents the increasing role of the modern fishes already occurring since the Middle Miocene in the wider Mediterranean area.

Acknowledgments. – It is a pleasure for us to thank Kristiaan Hoedemakers (RBINS) for improving the quality of the English of the present paper, and Adriano Vandersypen who did an important work in composing the tables.

REFERENCES

AGIADI K., TRIANTAPHYLLOU M., GIRONE A., KARAKITSIOS V. & DERMITZAKIS M., 2010. – Fish otolith paleobathymetric application to the Plio-Pleistocene deposits of Kephallonia and Zakynthos Islands (Ionian Sea, Western Greece). *Riv. Ital. Paleontol. Stratigr.,* 116(1): 63-78.

AGIADI K., TRIANTAPHYLLOU M., GIRONE A. & KARAKITSIOS V., 2011. – The Early Quaternary palaeobiogeography of the Eastern Ionian deep-sea Teleost fauna: a novel palaeocirculation approach. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 306(3-4): 228-242.

BAYKINA E.M. & SCHWARZHANS W.W., 2016. – Description of *Karaganops* n. gen. *perratus* (Daniltshenko 1970) with otoliths *in situ*, an endemic Karaganian (Middle Miocene) herring (Clupeidae) in the Eastern Paratethys. *Swiss J. Palaeontol.* 135(1): 1-12.

BRZOBOHATÝ R., 1981. – Zur Palökologie der fossilen Myctophiden (Myctophidae, Teleostei). *Západné Karpaty, Sér. Paleontol.,* 1981: 31-48.

BRZOBOHATÝ R., 1986. – Einige neue Arten von Knochenfischen (Teleostei, Otolithen) aus dem westkarpatischen Tertiär. *Acta Mus. Moraviae*, Sci. Nat., 71(1-2): 55-71.

BRZOBOHATÝ R., 1995. – Macrouridae (Teleostei, Otolithen) im Oligozän der Zentralen Paratethys und ihre paläogeographische Bedeutung. *Jb. Geol. Bundesanstalt, Wien* 138(4): 615-637.

BRZOBOHATÝ R., 1997. – Paleobathymetry of the Lower Badenian (Middle Miocene, Carpathian Foredeep, South Moraviaà based on otolith. In: Dynamics of Interaction between Marine and Continental Environements. (Hladilova S., ed.), pp. 37-45. Brno: Masaryk University Press. [in Czech, English abstract]

BRZOBOHATÝ R., 2001. – Paleogeography, paleobiogeography and bathymetry on fish, particularly otoliths. *Bericht. Inst. Geol. Paläontol. Karl-Franzens-Univ. Graz, Österreich*, 4: 37-40.

BRZOBOHATÝ R. & KRHOVSKÝ J., 1998. – A synopsis of the teleost taxa from the Pouzdrany Formation (West Carpathians, Pouzdrany Unit, Early Oligocene). *Zemni Plyn a Nafta,* 43(2): 279-289.

BRZOBOHATÝ R. & NOLF D., 1996. – Otolithes de myctophidés (poissons téléostéens) des terrains tertiaires d’Europe : révision des genres *Benthosema, Hygophum, Lampadena, Notoscopelus* et *Symbolophorus*. *Bull. Inst. R. Sci. Nat. Belg., Sci. Terre,* 66: 151-176.

BRZOBOHATÝ R. & NOLF D., 2000. – *Diaphus* otoliths from the European Neogene (Myctophidae, Teleostei). *Bull. Inst. R. Sci. Nat. Belg., Sci. Terre,* 70: 185-206.

BRZOBOHATÝ R. & NOLF D., 2002. – Stomiiformes (Teleostei, Otolithen) aus dem Miozän der Karpatischen Vortiefe (Westkarpaten, Mähren) und der Zentralen Paratethys. *Cour. Forschungsinst. Senckenb.,* 237: 139-150.

BRZOBOHATÝ R. & SCHULTZ O., 1978. – Die Fischfauna des Badeniens. *In*: M4. Badenien (Moravien, Wielicien, Kosovien) (Papp A., Cicha I., Seneš J. & Steininger F., eds), Chronostratigraphie und Neostratotypen 6, pp. 441-465. Bratislava: SAV Press.

BRZOBOHATÝ R. & STRÁNÍK Z., 2012. – Paleogeography of the Early Badenian connection between the Vienna Basin and the Carpathian Foredeep. *Cent. Europ. J. Geosci.* 4(1): 126-137.

BRZOBOHATÝ R., NOLF D. & KROUPA O., 2007. – Fish otoliths from the Middle Miocene of Kienberg at Mikulov, Czech Republic, Vienna Basin: their paleoenvironmental and paleogeographic significance. *Bull. Inst. R. Sci. Nat. Belg., Sci. Terre,* 77: 167-196.

CAMPANA S.E., 2004. – Photographic atlas of fish otoliths of the northwest Atlantic Ocean. *Canad. Spec. Publ. Fish. Aquat. Sci.,* 133: 1-284.

CHAINE J. & DUVERGIER J., 1928. – Sur les otolithes fossiles de la Pologne. *Rocz. Pol. Tow. Geol.* 5: 190-204.

CICHA I., BRZOBOHATÝ R., ČTYROKÁ J. *et al*. [14 authors], 1985. – Neogene in OS-1 Kravaře and OS-2 Hať key boreholes in the Opava area. *Sbor. Geol. Věd, Geol.* 40: 183-229. [in Czech, English abstract)]

COHEN D.M., INADA T., IWAMOTO T. & SCIALABA N., 1990. – Gadiform fishes of the world. FAO Species Catalogue, FAO Fisheries Synopsis 125 (10). Rome.

ĆORIĆ S. & ŠVÁBENICKÁ L., 2004. – Calcareous nannofossil biostratigraphy of the Grund Formation (Molasse Basin, Lower Austria). *Geol. Carpathica,* 54(2): 147-153.

DOLÁKOVÁ N., BRZOBOHATÝ R., HLADILOVÁ Š. & NEHYBA S., 2008. – The red-algal facies of the Lower Badenian limestones of the Carpathian Foredeep in Moravia (Czech Republic). *Geol. Carpathica,* 59(2): 133-146.

DOLÁKOVÁ N., HOLCOVÁ K., NEHYBA S., HLADILOVÁ Š., BRZOBOHATÝ R., ZÁGORŠEK K., HRABOVSKÝ J., SEKO M. & UTESCHER T., 2014. – The Badenian Parastratotype at Židlochovice from the perspective of the multiproxy study. *N. Jb. Geol. Paläontol., Abh.,* 271(2): 169-201.

FROESE R. & PAULY D. (eds), 2016. – FishBase. World Wide Web electronic publication. www.fishbase.org.version.

GIERL C. & REICHENBACHER B., 2015 – A new fossil genus of Gobiidae from the Miocene Characterised by a Mosaic Characters. *Copeia,* 103(4): 792-805.

GIRONE A., 2003. – The Pleistocene bathyal teleostean fauna of Archi (Southern Italy): Palaeoecological and Palaeobiogeographic implications. *Riv. Ital. Paleontol. Stratigr*., 109(1): 99-110.

GIRONE A., NOLF D. & CAPPETTA H., 2006. – Pleistocene fish otoliths from the Mediterranean Basin: a synthesis. *Geobios,* 39: 651-671.

GIRONE A., NOLF D. & CAVALLO O., 2010. – Fish otoliths from the pre-evaporitic (Early Messinian) sediments of northern Italy: their stratigraphic and paleobiogeographic significance. *Facies,* 56: 399-432.

HARDENBOL J., THIERY J., FARLEY M.B., JACQUIN T., GRACIANSKY P.C. & VAIL P.R., 1998. – Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins. *In*: Mesozoic and Cenozoic Sequence Stratigraphy of European Basins (Graciansky P.C., Hardenbol J., Jacquin T. & Vail P.R., eds). *SEPM Spec. Publ*., 60: 3-13.

HARZHAUSER M., MANDIĆ O. & ZUSCHIN M., 2003. – Changes in Paratethyan marine molluscs at the Early/Middle Miocene transition: diversity, palaeogeography and palaeoclimate. *Acta Geol. Pol.,* 53(4): 323-339.

HILGEN F.J, LOURENS L.J. & VAN DAM J.A., 2012. – The Neogene Period. *In*: The Geologic Time Scale 2012. 2 Volume Set, 1st Edit. (Gradstein F.M., Ogg J.G., Schmitz M.D. & Ogg G.M., eds), pp. 923-978. Amsterdam: Elsevier.

HOEDEMAKERS K. & BATLLORI J., 2005. – Fish otoliths from the Early and Middle Miocene of the Penedès (Catalunya, Spain). *Batalleria,* 12: 105-134.

HOHENEGGER J., ĆORIĆ S. & WAGREICH M., 2014. – Timing of the Middle Miocene Badenian stage of the Central Paratethys. *Geol. Carpathica,* 65(1): 55-66.

HOLCOVÁ K., BRZOBOHATÝ R., KOPECKÁ J., NEHYBA S., 2016. – Reconstruction of the unusual Middle Miocene (Badenian) palaeoenvironment of the Carpathian Foredeep (Lomnice/Tišnov denudational relict, Czech Republic). *Geol. Quart.,* 59(4): 654-678.

HUYGHEBAERT B. & NOLF D., 1979. – Otolithes de Téléostéens et biostratigraphie des Sables de Zonderschot (Miocène Moyen de la Belgique). *Meded. Werkgr. Tert. Kwart. Geol.,* 16(2): 59-100.

JARDAS I., 1996. – Adriatic Ichthyofauna. 533 p. Zagreb: Skolska knjiga.

KOKEN E., 1891. – Neue Untersuchungen an tertiären Fisch-Otolithen. II. *Zeitschr. Deutsch. Geol. Ges.,* 43: 77-170.

KOTLARCZYK J., JERZMANSKA A., SWIDNICKA E. & WISZNIOWSKA T., 2006. – A framework of ichthyofaunal ecostratigraphy of the Oligocene-Early Miocene strata of the Polish Outer Carpathian Basin. *Ann. Soc. Geol. Pol.,* 76: 1-111.

KOVÁČ M., ANDREYEVA-GRIGOROVICH A., BAJRAKTAREVIĆ Z. *et al.* [14 authors], 2007. – Badenian evolution of the Central Paratethys Sea: paleogeography, paleoclimate and eustatic changes. *Geol. Carpathica,* 58(6): 579-606.

LIN C.H., GIRONE A. & NOLF D., 2015. – Tortonian fish otoliths from turbiditic deposits in northern Italy: taxonomic and stratigraphic significance. *Geobios,* 48: 249-261.

LIN C.H., GIRONE A. & NOLF D., 2016. – Fish otolith assemblages from Recent NE Atlantic sea bottoms: A comparative study of palaeoecology. *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 446: 98-107.

LIN C.H., BRZOBOHATÝ R., NOLF D. & GIRONE A., 2017. – Tortonian teleost otoliths from Northern Italy: taxonomic synthesis and stratigraphic significance. *Eur. J. Taxon.,* 322: 1-44.

MARTINI E., 1971. – Standard Tertiary and Quaternary Calcareous Nannoplankton Zonation. Proc. 2nd Plankt. Conf., Roma, 1970. Ed. Technoscienza, 2: 739-785.

NAFPAKTITIS B.G., BACKUS R.H., CRADDOCK J.E., HAEDRICK R.L., ROBINSON B.H. & KARNELLA C., 1977. – Family Myctophidae. *In*: Fishes of the Western North Atlantic (Tee Van J., ed.). *Sears Found. Mar. Res., Mem.,* 1(7): 13-265.

NEAR T.J., EYTAN R.I., DORNBURG A., KUHN K.L., MOORE J.A., DAVIS M.P., WAINWRIGHT P.C., FRIEDMAN M. & SMITH W.L., 2012. – Resolution of ray-finned fish phylogeny and timing of diversification. *Proc. Nat. Acad. Sci. U.S.,* 109(34): 13698-13703.

NELSON J.S., 2006. – Fishes of the World. 4th edit., 601 p. New York: John Wiley & Sons.

NOLF D., 1981. – Révision des types d'otolithes de poissons fossiles décrits par R. Schubert. *Verhandl. Geol. B.-A.,* (2): 133-183.

NOLF D., 1985. – Otolithi Piscium. *In*: Handbook of Paleoichthyology, 10 (Schultze H.P., ed.). 145 p. Stuttgart and New York: Fischer.

NOLF D., 2013. – The diversity of fish otoliths, past and present (Steurbaut E., Brzobohaty R. & Hoedemakers K., eds). 222 p., 359 Pl. Brussels: Royal Belgian Institute of Natural Sciences.

NOLF D. & BRZOBOHATÝ R., 1994a. – Fish otoliths as paleobathymetric indicators. *Paleontol. Evol.,* 24-25(1992): 255-264.

NOLF D. & BRZOBOHATÝ R., 1994b. – Fish otoliths from the Late Oligocene (Eger and Kiscell Formations) in the Eger area (northeastern Hungary). *Bull. Inst. R. Sci. Nat. Belg., Sci. Terre,* 64: 225-252.

NOLF D. & BRZOBOHATÝ R., 2002. – Otolithes de poissons du Paléocanyon de Saubrigues (Chattien à Langhien), Aquitaine méridionale, France. *Rev. Micropaléontol.,* 45(4): 261-296.

NOLF D. & BRZOBOHATÝ R., 2009. – Lower Badenian fish otoliths of the Styrian and Lavanttal basins, with a revision of Weinfurter's type material. *Ann. Naturhistor. Mus. Wien,* 111A: 323-356.

NOLF D. & CAPPETTA H., 1989. – Otolithes de poissons pliocènes du Sud-Est de la France. *Bull. Inst. R. Sci. Nat. Belg., Sci. Terre,* 58(1988): 209-271.

NOLF D. & STEURBAUT E., 1983. – Révision des otolithes de téléostéens du Tortonien stratotypique et de Montegibbio (Miocène supérieur de l'Italie septentrionale). *Meded. Werkgr. Tert. Kwart. Geol.,* 20(4): 143-197.

NOLF D. & STEURBAUT E., 1988. – Description de la première faune ichtyologique exclusivement bathyale du Tertiaire d'Europe: otolithes de l'Oligocène Inférieur du gisement de Pizzocorno, Italie septentrionale. *Bull. Inst. R. Sci. Nat. Belg., Sci. Terre,* 57: 217-230.

NOLF D. & STEURBAUT E., 1989. – Evidence from otoliths for establishing relationships within gadiforms. *In*: Papers on the Systematics of Gadiform Fishes (Cohen D.M., ed.), Sci. ser. 32, pp. 89-111. Los Angeles County Natural History Museum.

NOLF D., STEURBAUT, E., 2004. – Otolithes de poissons de l'Oligocène inférieur du Bassin liguro-piémontais oriental, Italie. *Riv. Piemont. Stor. Nat.*, 25: 21-68.

NOLF D. & TYLER J.C., 2006. – Otolith evidence concerning interrelationships of caproid, zeiform and tetraodontiform fishes. *Bull. Inst. R. Sci. Nat. Belg., Biol.,* 76: 147-189.

OHE F., 1985. – Marine fish-otoliths of Japan. *Spec. Vol. Bull. (Earth-Science), Aichi Univ. Educ.,* 1-184.

OSZCZYPKO N. & OSZCZYPKO-CLOWES M., 2012. – Stages of development in the Polish Carpathian Foredeep basin. *Cent. Eur. J. Geosci.,* 4: 138-162.

PAPP A., CICHA I., SENEŠ J. & STEININGER F., 1978. – M4, Badenien (Moravien, Wielicien, Kosovien), Chronostratigraphie und Neostratotypen 6. 594 p. Bratislava: SAV Press.

PROCHÁZKA V.J., 1892a. – Vorläufiger Bericht über die stratigraphischen und faunistischen Verhältnisse des westlichen Miocaengebietes von Mähren. *Věst. Král. čes. spol. nauk* 1892: 326-368.

PROCHÁZKA V.J., 1892b. – Zur Stratigraphie der Oncophora-Sande der Umgebung von Ivančic und Oslavan in Mähren. *Věst. Král. čes. spol. nauk* 1892: 425-457.

PROCHÁZKA V.J., 1892c. – Moravian Miocene. *Věst. Král. čes. spol. nauk* 1892: 458-475. [In Czech]

PROCHÁZKA V.J., 1892d. – Ein Beitrag zur Kenntniss der Fauna des Miozängebietes der Umgebung von Mährische Trübau. *Verhandl. k.-k. Geol. R.-A.,* 5: 100-107.

PROCHÁZKA V.J., 1893a. – Das Miozän von Seelowitz in Mähren und dessen Fauna. *Rozpr. Čes. Akad. Cís. Fr. Josefa Slov. Umení v Praze,* 2(2): 65-88.

PROCHÁZKA, V.J., 1893b. Über die Fauna der durch das Bohrloch nächst Gross-Opatowitz durchteuften Neogengebilde. *Jb. k.-k. Geol. R.-A.,* 43(1): 125-132.

PROCHÁZKA V.J., 1894. – Das Miozän von Kralice nächst Námest in Mähren. *Sitzungsber. Kön. Böhm. Ges. Wiss. Math.-Naturwiss. Cl.,* 1893: 1-71.

PROCHÁZKA V.J., 1899. – Miocene deposits in the Moravian Karst. *Rozpr. Čes. Akad. Cís. Fr. Josefa Vědy, Slov. Umění v Praze,* 8(41): 1-37. [In Czech]

PROCHÁZKA V.J., 1900. – Das ostböhmische Miocaen. *Arch. Naturwiss. Durchforsch. Böhmens,* 10(2): 77-86.

PŘIKRYL T., BRZOBOHATÝ R. & GREGOROVÁ R., 2016. – Diversity and distribution of fossil codlets (Teleostei, Gadiformes, Bregmacerotidae): review and commentary. *Palaeobiodiv. Palaeoenviron.,* 96: 13-39.

QUÉRO J.C., PORCHÉ P. & VAYNE J.J., 2003. – Guide des Poissons de l'Atlantique européen. 465 p. Lonay (Switzerland): Delachaux et Niestlé S.A.

RADWANSKA U., 1992. – Fish otoliths in the Middle Miocene (Badenian) deposits of southern Poland. *Acta Geol. Pol.,* 42(3-4): 141-328.

RIVATON J. & BOURRET P., 1999. – Les otolithes des poissons de l'Indo-Pacifique. Documents scientifiques et techniques. *IRD Nouméa,* 2(2): 1-378.

ROBBA E., 1970. – Otoliti del Tortoniano-tipo (Piemonte). *Riv. Ital. Paleontol.,* 76(1): 89-172.

RÖGL F., 1998. – Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Ann. Naturhistor. Mus. Wien,* 90A: 279-310.

RÖGL F. & SPEZAFFERRI S., 2003. – Foraminiferal paleoecology and biostratigraphy of the Mühlbach section (Gaindorf Formation, Lower Badenian) Lower Austria. *Ann. Naturhistor. Mus. Wien,* 104A: 23-75.

SCHUBERT R.J., 1905. – Die Fischotolithen des österr.-ungar. Tertiärs. II. Macruriden und Beryciden. *Jb. k.-k. Geol. R.-A. Wien,* 55: 613-638.

SCHUBERT R.J., 1906. Die Fischotolithen des österr.-ungar. Tertiärs. III. *Jb. k.-k. Geol. R.-A. Wien,* 56: 623-706.

SCHULTZ O., 2003. – The Middle Miocene Fish Fauna (excl. otolithes) from Mühlbach am Manhartsberg and Grund near Hollabrunn, Lower Austria. *Ann. Naturhistor. Mus. Wien*, 104 A: 185-193.

SCHULTZ O., 2013. – Pisces. *In*: Catalogus Fossilium Austriae 3, pp. 1-567. Wien: Verlag der Oesterreichischen Akademie der Wissenschaften.

SCHWARZHANS W., 1986. – Die Otolithen des Unter-Pliozän von Le Puget, S-Frankreich. *Senckenberg. Leth.,* 67(1-3): 219-273.

SCHWARZHANS W., 1999. – A comparative morphological treatise of recent and fossil otoliths of the Order Pleuronectiformes. *In*: Piscium Catalogus, Part Otolithi Piscium 2, pp. 1-391, München: Verlag Dr. Fiedrich Pfeil.

SCHWARZHANS W., 2010. – The Otoliths from the Miocene of the North Sea Basin. 352 p. Leiden: Backhuys Publishers, Weikersheim: Margraf Publishers.

SCHWARZHANS W., 2013. – Otoliths from dredges in the Gulf of Guinea and off the Azores – an actuo-paleontological study. *Palaeo Ichthyol.,* 13: 7-40.

SCHWARZHANS W., 2014. – Otoliths from the middle Miocene (Serravallian) of the Karaman Basin, Turkey. *Cainozoic Res.,* 14(1): 35-69.

SMALE J.M., WATSON G. & HECHT T., 1995. – Otolith atlas of southern African marine fishes. *Ichthyolog. Monogr. J.L.B. Smith Inst. Ichthyol.,* 1: 1-253.

SMIGIELSKA T., 1966. – Otoliths of fishes from the Tortonian of Southern Poland. *Ann. Soc. Géol. Pol.,* 36: 205-275.

SMIGIELSKA T., 1973. – Fish otoliths from the Lower Tortonian deposits at Niskowa near Nowy Sacz. *Ann. Soc. Géol. Pol.,* 43(1): 3-40.

SMIGIELSKA T., 1979. – Fish otoliths from the Korytnica clays (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Pol.,* 29(3): 295-336.

STEURBAUT E., 1984. – Les otolithes de téléostéens de l'Oligo-Miocène d'Aquitaine (Sud-Ouest de la France). *Palaeontographica* A, 186(1-6): 1-162.

SWAN S.C. & GORDON J.D.M., 2001. – A review of age estimation in macrourid fishes with new data on age validation of juveniles. *Fish. Res.,* 51(2-3): 177-195.

WADE B.S., PEARSON P.N., BERGGREN P.N., PÄLIKA H., 2011. – Review and revision of Cenozoic tropical planctonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical timescale. *Earth-Sci. Rev.,* 104: 11-142.

WEILER W., 1950. – Die Otolithen aus dem Jungtertiär Süd-Rumäniens. 2. Mittel-Miozän, Torton, Buglow und Sarmat. *Senckenberg. Leth.,* 31: 209-258.

WEINFURTER E., 1952. – *In*: Papp A.: Zur Kenntnis des Jungtertiärs in der Umgebung von Krems a.d. Donau (N-Ö). *Verhandl. geol. B.-A. Wien,* 1952(3): 1-5.