Swiss J Palaeontol (2017) 136:1–6
DOI 10.1007/s13358-017-0126-9

Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Preface: a first attempt to fill the gap between the otolith and skeletal records of teleost fishes

Werner Schwarzhans[1] · **Giorgio Carnevale**[2]

Received: 18 December 2016 / Accepted: 10 January 2017 / Published online: 11 March 2017

Abstract The studies presented in this special issue describe and evaluate otoliths in situ in 18 species of extinct Paratethyan fishes, 17 from Sarmatian, and one from Karaganian deposits. Together with previously described fishes from the area with otoliths in situ and additional works which we are aware of being in progress, this time interval has now yielded 34 fish species with otoliths in situ, approximately equivalent to one-third of the entire Sarmatian fish fauna of the Paratethys known to date. Therefore, it represents by far the most diverse fossil fish fauna with otoliths in situ. The implications of the linking of skeletal and otolith data are briefly discussed as well as the prospects for future research. The anecdotal history of the formation of the work group which became engaged in these studies is presented.

Keywords Otoliths in situ · Articulated fish skeletons · Palaeo-ichthyology · Miocene · Paratethys

Articulated fish skeletons with otoliths in situ are the necessary ingredients to link these two data sets which have been traditionally treated separately. The link is generally considered to be rare and occasional. This was also our idea, when a few years ago, we exchanged our views about a long forgotten gadid fish originally described from the Badenian of Austria by Kner in 1862—*Palimphemus anceps*. Giorgio Carnevale at that time reappraised *Palimphemus anceps* in cooperation with Mathias Harzhauser and Ortwin Schultz (Carnevale et al. 2012). Werner Schwarzhans recalled of an articulated gadid fish specimen kept at the Wrocław University in Poland with an otolith in situ. A detailed analysis of this articulated skeleton revealed that it also represents *Palimphemus anceps*. Even more exciting, it helped to synonymize the otolith-based species *Colliolus sculptus* (Koken 1891) with the skeleton-based *Palimphemus anceps* Kner 1862, thereby eradicating a case of more than 100 years of parallel taxonomy (Schwarzhans 2014). This result inspired us to look for additional cases allowing the correlation between skeleton- and otolith-based taxonomy, which we both feel is absolutely necessary. Our attention then became attracted by comments found in Schubert (1906) about otoliths in situ he had seen in ten different species of articulated skeletons from the collection of Sarmatian fishes from Dolje near Zagreb, Croatia assembled by Dragutin Kramberger. Katarina Bradić contacted Werner to discuss the identity of certain otoliths found in the vicinity of Belgrade, Serbia (Schwarzhans et al. 2015). This in turn led to approach Sanja Japundžić in Zagreb, Croatia, where most of the Karmberger's specimens are kept in the collection of the Croatian Natural History Museum (CNHM). Katarina Bradić also informed us that she had identified a number of fishes with otoliths in situ in the collection assembled and studied by Jelena S. Anđelković from the Sarmatian of Belgrade housed at the Chair of Historical Geology, Department of Regional Geology, Faculty of Mining and Geology, and University of Belgrade (RGF). Werner Schwarzhans traveled to Zagreb to meet Sanja Japundžić and examine the Kramberger's fishes, and to Belgrade to meet Katarina Bradić

Editorial handling: Daniel Marty.

✉ Werner Schwarzhans
wwschwarz@aol.com

[1] Natural History Museum of Denmark, Zoological Museum, Universitetsparken 15, 2100 Copenhagen, Denmark

[2] Dipartimento di Scienze della Terra, Università degli Studi di Torino, via Valperga Caluso 35, 10125 Turin, Italy

Table 1 List of Sarmatian and Karaganian/Konkian species with otoliths in situ, including a list of reviewed skeleton-based species and a list containing reviewed isolated otolith-based species

Lower Sarmatian s.s. (Volhynian)		
Species with otoliths in situ	Revisions: skeleton-based	Revisions: otolith-based and isolated otoliths
Clupeidae		
***Moladivchthys switshenskae* Baykina & Schwarzhans 2017**	*Clupea humilis* H.v.Meyer 1851 (senso Ionko 1954)	
***Sarmatella doljeana* (Kramberger 1883)**		
***Sarmatella tsurevica* (Baykina 2012)**		
Gadidae		
***Palimphemus macropterygius* (Kramberger 1883)**	*Gadus macropterygius* (Kramberger 1883)	*Palimphemus minusculoides* (Schubert 1912)
Palimphemus sp.*	*Micromesistius* sp.	
***Paratrisopterus caspius* (Bogatshov 1929)**	*Gadus caspius* Bogatshov 1929	*Paratrisopterus insectus* (Weiler 1943)
	Properca sabbai Pauca 1929 (sensu Anđelković 1969)	*Ot. (Macruridarum) acuminatus* Weiler 1943
	Paratrisopterus avus Fedotov 1971	*Ot. (Macruridarum) ovalis* Weiler 1943
	Gadus lanceolatus (Kramberger 1883) (sensu Anđelković 1989)	? *Paratrisopterus irregularis* Gaemers 1973
Lotidae		
***Enchelyopus susedanus* (Kner 1863)**	*Brosmius susedanus* Kner 1863 *Brosmius elonqatus* Kramberqer 1883	*Enchelyopus susedanus* (Kner 1863)
Atherinidae		
***Atherina suchovi* Switshenska 1973**		
Scorpaenidae		
***"Scorpaena" minima* Kramberger 1882**		
Moronidae		
Morone ionkoi Bannikov 1993		
Sparidae		
Pshekharus yesinorum Bannikov & Kotlyar 2015		
Sparus insignis (Prochazka 1893)		*Sparus insignis* (Prochazka 1893)
Labridae		
Symphodus salvus Bannikov 1983		
***Symphodus woodwardi* (Kramberger 1891)**		
Callionymidae		
Callionymus macrocephalus Kramberger 1882*		*Callionymus primus* Weiler 1943
Trachinidae		
Trachinus sp.*		
Clinidae		
Clinitrachoides gratus (Bannikov 1989)		
Gobiidae		
***Aphia macrophthalma* Schwarzhans, Ahnelt, Carnevale & Japundžić 2017**		
***Economidichthys triangularis* (Weiler 1943)**		*Economidichthys triangularis* (Weiler 1943)
***Hesperichthys reductus* Schwarzhans, Ahnelt, Carnevale & Japundžić 2017**		*Hesperichthys reductus* Schwarzhans et al. 2017c
Gobius elatus Steindachner 1860**		
Gobius viennensis Steindachner 1860**		
Pomatoschistus sp.*		

Table 1 continued

Lower Sarmatian s.s. (Volhynian)		
Species with otoliths in situ	Revisions: skeleton-based	Revisions: otolith-based and isolated otoliths
***Proneogobius pullus* (Kramberger 1882)**	*Gobius pullus* Kramberger 1882	
***Protobenthophilus squamatus* Schwarzhans, Ahnelt, Carnevale & Japundžić 2017**		*Protobenthophilus squamatus* Schwarzhans et al. 2017c
Gobiesocidae		
***Apletodon* sp.**		
Bothidae		
***Arnoglossus bassanianus* (Kramberger 1883)**	*Rhombus bassanianus* Kramberger 1883	*Arnoglossus? tenuis* (Schubert 1906) *Rhombus corius miocenicus* Pobedina 1954 *Rhombus corius foliformis* Pobedina 1954
***Bothus parvulus* (Kramberger 1883)**	*Rhombus parvulus* Kramberger 1883	
Bothus sp.*		
Soleidae		
***Parasolea serbica* (Anđelković 1966)**	*Rhombus serbicus* Anđelković 1966 *Rhombus stamatini* Pauca 1931 (senso Anđelković 1969)	*Parasolea serbica* (Anđelković 1966)

Konkian and Karaganian		
Species with otoliths in situ	Revisions: skeleton-based	Revisions: otolith-based and isolated otoliths
Clupeidae		
***Karaganops perratus* (Daniltshenko 1970)**	*Sardinella perrata* Daniltshenko 1970	
Bregmacerotidae		
Bregmaceros albyi (Sauvage, 1880)		*Bregmaceros albyi* (Sauvage, 1880)
Gadidae		
Palimphemus anceps Kner 1862	*Gadus lanceolatus* (Kramberger 1883)	*Colliolus sculptus* (Koken 1891) *Gadus friedbergi* Chaine & Duvergier 1928 *Gadus schuberti* Smigieldska 1966 *Colliolus johannettae* Gaemers 1976 *Pseudocolliolus eidelstedtensis* Gaemers 1987 *Circagadiculus swalmensis* Gaemers 1990 *Colliolus septentrionalis* Gaemers 1990
Callionymidae		
Protonymus gontsharovae Sytchevskaya & Prokofiev 2007		

Annotations in "Species with otoliths in situ" column: bold = species described in articles of this special volume; * = species currently under study by Giorgio Carnevale and Alexandre F. Bannikov; and ** = species currently under study by Christoph Gierl and Bettina Reichenbacher

and see the Anđelković material. The amount of data was overwhelming and the quartet agreed to realize a series of contributions dealing with the Sarmatian fishes with otoliths in situ from those two collections (Schwarzhans et al. 2017a, b, c, d, e). During the preparation of the various articles, further colleagues were invited to participate: Alexandre F. Bannikov, who made available specimens of *Atherina suchovi* with otoliths in situ from the Sarmatian of Moldavia (Schwarzhans et al. 2017a), Andriy Bratishko for his expertise in otoliths from the Miocene of the Eastern Paratethys (Bratishko et al. 2015, and Schwarzhans et al. 2017b, c) and Harald Ahnelt for his expertise in gobies of the Ponto-Caspian Basin (Schwarzhans et al. 2017c). During a trip to Moscow in the same year, Werner met with Eugenia Baykina, who was reviewing the fossil clupeids from the Paratethys. She found two clupeid species containing otoliths in situ among her material and it was decided to separately describe them (Baykina and Schwarzhans 2017a, b). The scope and format were agreed by the group when the editor of the Swiss Journal of Palaeontology proposed to publish these articles in a special issue of the journal dealing with otoliths in situ.

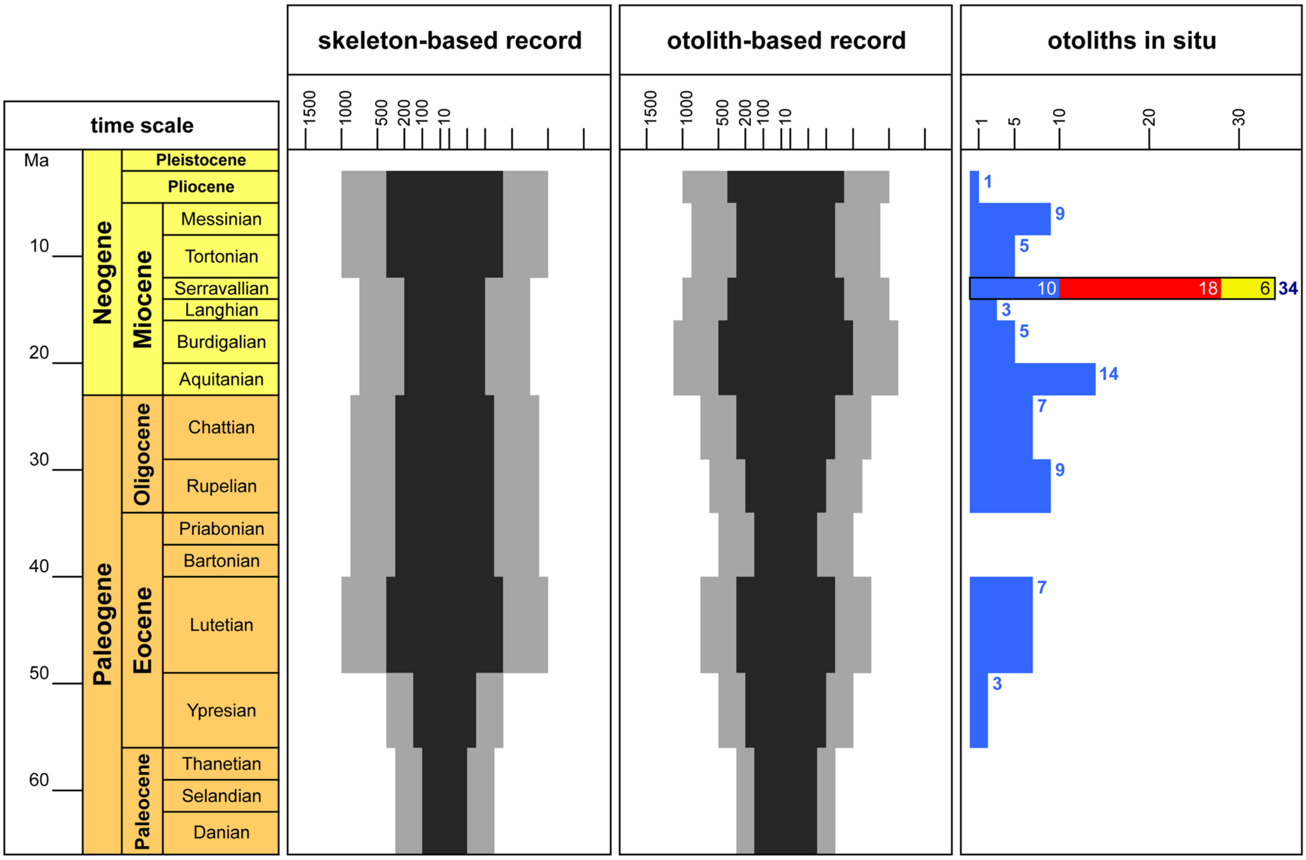

Fig. 1 Cenozoic chronological correlation chart of teleost diversity as based on articulated skeletons and otoliths, and number of species described with otoliths in situ. *Scale bars* in skeleton-based record: *Black* minimum count as based on Bannikov (2010) (Cenozoic of the CIS); Fierstine et al. (2012) (Cenozoic of California); Friedman et al. (2015) (London Clay); and Carnevale et al. (2014) (Monte Bolca) and various authors for the Miocene of Italy and Algeria. *Grey* best estimate count. *Scale bars* in otolith record: *Black* minimum count as based on Nolf, (2013). *Grey* best estimate count, including post 2013 data and estimation by one of us (WS). *Scale bars* in otoliths in situ record: *Blue* published, *Red* this volume, and *Yellow* currently under study

The initial concept was to focus on the otoliths in situ and their correlation with isolated otoliths, with a limited revisionary work of articulated skeletons (Schwarzhans et al. 2017a). However, most of the fishes formerly studied by Kramberger and Anđelković have never been reviewed and it was soon recognized that our concept was unsatisfying. For instance, we found that the number of nominal species of the Gadidae, Lotidae, and probably also Clupeidae was exaggerated, while a single species of the Gobiidae described by Kramberger turned out to represent five different species belonging to five different genera, and finally, we identified the first fossil record of the family Gobiesocidae. Seventeen species of Sarmatian fishes and one from the Karaganian were found to contain otoliths in situ. Eleven of those are also known from isolated otoliths, including eight otolith-based species as junior synonyms. Two species—*Sparus insignis* (Prochazka 1893) (in Brzobohaty 1979) and *Economidichthys triangularis* (Weiler 1943) (in Schwarzhans et al. 2017c)—were first established by means of otoliths. Seven additional Sarmatian fish species have been previously described with otoliths in situ as well as three additional taxa from the Karaganian and Konkian. Furthermore, we are aware of studies currently under way by Giorgio Carnevale and Alexandre F. Bannikov (see Carnevale et al. 2006) and by Christoph Gierl and Bettina Reichenbacher (see Gierl and Reichenbacher 2015) containing at least six further Sarmatian fish species with otoliths in situ.

Overall, up to 30 Sarmatian or, more generally, 34 Middle Miocene fish species with otoliths in situ are now recognized from the Central and Eastern Paratethys (Table 1). These data clearly indicate that this represents by far the most diverse fossil fish fauna with linked skeletons and otoliths known to date (Fig. 1). About one-third of all the valid Sarmatian fish species are now recorded with otoliths in situ. Carnevale et al. (2006) and Bannikov (2010) noted that fishes from the Sarmatian of Russia and Moldavia often contain otoliths in situ. A similar pattern is also evident for the fishes from Dolje in Croatia and Belgrade in Serbia.

The articles presented in this special issue document the power of coherent integrated data that result from such investigations. First and foremost, the study of isolated otoliths is significantly enhanced by the link with skeletal material. Articulated fish skeletons offer a relevant amount of characters for systematic and phylogenetic analyses compared to otoliths, and therefore, otoliths in situ are essential for calibrating isolated otolith finds in the sedimentary record. This becomes ever more important for ancient geological times when allocation of isolated otoliths becomes increasingly ambiguous. Such calibration points will also help to better interpret non-linked otolith-based species. On the other hand, otoliths in situ also aid in the assessment of skeletal finds by offering valuable additional taxonomic information, as, for instance, shown here in the articles dealing with clupeids, gobies, and soleids. Furthermore, isolated otoliths are generally so much more common in the fossil record than identifiable articulated skeletons that they considerably enhance the understanding of the distribution of fossil fishes in space and time. Finally, we have also demonstrated that skeletal fish remains and isolated otoliths do not strictly duplicate and that in addition to many instances of a good correlation, there are also instances, where they complement each other.

Our experience with the otoliths in situ in Sarmatian fishes of the Paratethys convinced us that otoliths in situ may prove not to be as rare as often believed. We hope that the studies presented here will inspire many colleagues to look out for more of these cases and undertake many more studies that link the taxonomy of fossil articulated skeletal remains and otoliths.

Acknowledgements We are extremely grateful to many colleagues who have supported our studies with specific advice, support in comparative material, tracing of material, preparation of photographs, and stratigraphic information: Christoph Gierl and Bettina Reichenbacher (München), Rostislav Brzobohaty (Brno), Jørgen Nielsen and Peter Møller (København), Ekaterina Vasilieva and Artem Prokofiev (Moscow), Strashimir Strashimirov, Dimka Sinnyovska and Elena Koleva (Sofia), Ljupko Rundić (Beograd), Bruno Chanet (Paris), and Ortwin Schultz (Wien). More generally, thanks are also due to many institutions that have provided access to extracting otoliths from Recent fishes over many years to one of us (WS), e.g., Australian Museum, Sydney (AMS), Natural History Museum, London (BMNH), Kochi University, Department of Biology, Faculty of Science, Kochi (BSKU), California Academy of Science, San Francisco (CAS), Los Angeles County Museum of Natural History, Los Angeles (LACM), Muséum National d'Histoire Naturelle, Paris (MNHN), National Science Museum, Department of Zoology, Tokyo (NSMT), National Museum of Natural History, Smithsonian Institution, Washington (USNM), Western Australian Museum, Perth (WAM), Universität Hamburg, Zoologisches Institut und Museum, Hamburg (ZMH), Zoological Museum, Moscow State University, Moscow (ZMMSU), Zoological Museum, and University of Copenhagen, Copenhagen (ZMUC). We sincerely thank our coauthors for their most valuable contributions: Sanja Japundžić (Zagreb), Katarina Bradić (Beograd), Alexandre Bannikov (Moscow), Eugenia Baykina (Moscow), Andriy Bratishko (Luhansk), and Harald Ahnelt (Wien). The research of GC was supported by grants (ex-60% 2014, 2015 and 2016) from the Università degli Studi di Torino. We thank the various reviewers of our individual articles for their constructive criticisms of earlier versions of the respective manuscripts. Finally, we wish to thank the responsible editors of the Swiss Journal of Palaeontology, Daniel Marty (Basel) and Lionel Cavin (Geneva) for their valuable support.

References

Bannikov, A.F. (2010). *Fossil vertebrates of Russia and adjacent countries. Fossil Acanthopterygian fishes* (*Teleostei, Acanthopterygii*) (pp. 1–244). Moscow: Russian Academy of Sciences, Borissiak Paleontological Institute, Geos (in Russian).

Baykina, E. M. & Schwarzhans, W. (2017a). Description of *Karaganops* n. gen. *perrata* (Daniltshenko, 1970) with otoliths in situ, an endemic Karaganian (Middle Miocene) hering (Clupeidae) in the Eastern Paratethys. *Swiss Journal of Palaeontology*. doi:10.1007/s13358-016-0115-4.

Baykina, E. M. & Schwarzhans, W. (2017b). Review of "*Clupea humilis*" from the Sarmatian of Moldova and description of *Moldavichthys switshenskae* gen. et sp. nov. *Swiss Journal of Palaeontology*. doi:10.1007/s13358-016-0121-6.

Bratishko, A., Schwarzhans, W., Reichenbacher, B., Vernihorova, Y., & Ćorić, S. (2015). Fish otoliths from the Konkian (Miocene, early Serravallian) of Mangyshalk (Kazakhstan)- testimony of an early endemic evolution in the Eastern Paratethys. *Paläontologische Zeitschift, 89,* 839–889.

Brzobohaty, R. (1979). *Sparus insignis* (Prochazka, 1893) (Pisces, Teleostei) otolity in situ ze svrchniho bádenu Opavska. *Casopis Slezského Muzea v Opave, A, 23,* 167–177.

Carnevale, G., Bannikov, A. F., Landini, W., & Sorbini, C. (2006). Volhynian (early Sarmatian s.l.) fishes from Tsurevsky, North Caucasus (Russia). *Journal of Paleontology, 80,* 684–699.

Carnevale, G., Bannikov, A. F., Marramà, G., Tyler, J. C., & Zorzin, R. (2014). The Pesciara-Monte Postale *Fossil Lagerstätte*: 2. Fishes and other vertebrates. In C. A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi, & R. Zorzin (eds.), The Bolca *Fossil Lagerstätten*: A window into the Eocene World. *Rendiconti della Società Paleontologica Italiana* (vol. 4, pp. 37–63).

Carnevale, G., Harzhauser, M., & Schultz, O. (2012). The Miocene gadid fish *Palimphemus anceps* Kner, 1862: a reappraisal. *Geodiversitas, 34,* 625–643.

Fierstine, H. L., Huddleston, R. W., & Takeuchi, G. T. (2012). Catalog of the Neogene bony fishes of California. A systematic inventory of all published accounts. *Occasional papers of the California Academy of Sciences, 159,* 1–206.

Friedman, M., Beckett, H. T., Close, R. A., & Johanson, Z. (2015). The English Chalk and London Clay: two remarkable British bony fish Lagerstätten. *Geological Society, London, Special Publications, 430,* 165–200.

Gierl, C., & Reichenbacher, B. (2015). A new fossil genus of Gobiiformes from the Miocene characterized by a mosaic set of characters. *Copeia, 103*(4), 792–805.

Nolf, D. (2013). *The Diversity of Fish Otoliths, Past and Present* (p. 222). Brussels: Royal Belgian Institute of Natural Sciences.

Schubert, R. J. (1906). Die Fischotolithen des österr.-ungar. Tertiärs III. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt, 56,* 623–706.

Schwarzhans, W. (2014). Synonymisation of the skeleton-based *Palimphemus anceps* Kner 1862 and the otolith-based *Colliolus sculptus* (Koken 1891) (Pisces, Teleostei, Gadidae). *Cainozoic Research, 14,* 9–16.

Schwarzhans, W., Bradić, K., & Lj, Rundić. (2015). Fish-otoliths from the marine-brackish water transition from the Middle Miocene of the Belgrade area, Serbia. *Palaontologische Zeitschift, 89*(4), 815–837.

Schwarzhans, W., Carnevale, G., Bannikov, A.F., Japundžić, S. & Bradić K. (2017a). Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part I: *Atherina suchovi* Switchenska, 1973. *Swiss Journal of Palaeontology*, *136*(1). doi:10.1007/s13358-016-0114-5 (in this issue).

Schwarzhans, W., Carnevale, G., Bratishko, A., Japundžić, S. & Bradić K. (2017b). Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part II: Gadidae and Lotidae. *Swiss Journal of Palaeontology*, *136*(1). doi:10.1007/s13358-016-0114-5 (in this issue).

Schwarzhans, W., Ahnelt, H., Carnevale, G., Japundžić, S., Bradić, K., & Bratishko, A. (2017c). Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part III: tales from the cradle of the Ponto-Caspian gobies. *Swiss Journal of Palaeontology*, *136*(1). doi:10.1007/s13358-016-0120-7 (in this issue).

Schwarzhans, W., Carnevale, G., Japundžić, S. & Bradić-Milinović K. (2017d). Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part IV: Scorpaenidae, Labridae, and Gobiesocidae. *Swiss Journal of Palaeontology*, *136*(1). doi:10.1007/s13358-017-0124-y (in this issue).

Schwarzhans, W., Carnevale, G., Japundžić, S. & Bradić K. (2017e). Otoliths in situ from Sarmatian (Middle Miocene) fishes of the Paratethys. Part V: Bothidae and Soleidae. *Swiss Journal of Palaeontology*, *136*(1). doi:10.1007/s13358-017-0128-7 (in this issue).