The fish fauna of the Dynów Marl Member (Menilite Formation, Poland): paleoenvironment and paleobiogeography of the early Oligocene Paratethys

MAŁGORZATA BIEŃKOWSKA-WASILUK

The Dynów Marl Member of the Menilite Formation in Poland is one of the most significant lithostratigraphic units containing fauna of the early Oligocene Paratethys. The fish fauna from this member is presented, including three shark taxa and eight teleost taxa. The connection between the Upper Rhine Graben and the Central Paratethys in the calcareous nannoplankton zone NP23 (about 30–32 Ma ago) is consistent with the occurrence of the teleost Anenchelum glarisanum and the shark Keasius parvus. The presence of the teleosts Scopeloides glarisanus, Vinciguerria obscura and Oligophus moravicus confirms the connections between the Eastern and Central Paratethys. The distribution of the ichthyofauna supports the existence of a marine connection between the North Sea, the Upper Rhine Graben, the northwestern Tethys, and the Central and Eastern Paratethys during the early Oligocene. The fish assemblage shows a high percentage of fishes, whose extant relatives are living in the depth interval between 0 and 500 m. The presence of Gonostomatidae, Phosichthyidae and Myctophidae indicates normal salinity in the deep pelagic life zones. The fish fauna show distinctly Paratethyan affinities. • Key words: Teleostei, Elasmobranchii, Rupelian, Outer Carpathians.


Małgorzata Bieńkowska-Wasiluk, Faculty of Geology, University of Warsaw, Żwirki i Wigury 93, 02-089 Warsaw, Poland; m.wasiluk@uw.edu.pl

Origin of the Paratethys is defined by the presence of endemic bivalve fauna inhabiting newly formed semi-closed basin, correlated with the early Oligocene nannoplankton zone NP23 (Martini 1971, Studencka et al. 2016). The isolation of the basin was noticeably influenced by the global cooling during the Cenozoic and the convergence between the European and Adriatic (African) plates (Rusu 1977, 1988; Băldi 1989; Kovač et al. 1994, 1997, 2016, 2017; Rögl 1998, 1999; Meulenkamp et al. 2000; Steininger & Wessely 2000; Popov et al. 2002; Schulz et al. 2004). Many authors have correlated the origin of the Paratethys with the Eocene–Oligocene boundary and particular factors indicating the isolation of the basin (Schulz et al. 2005; Sachsenhofer et al. 2017).

The deposition period of the Dynów Marl Member of the Menilite Formation in Poland covers a part of NP23, which was a significant period of the early Paratethys. The diverse assemblage of fish provides an essential insight into the paleoenvironment of the Central Paratethys and is of particular importance, because it contains fauna with a wide distribution, from the Upper Rhine Graben to the Eastern Paratethys. Lists of the fish fauna from this member have been presented by Kotlarczyk et al. (2006), and Bieńkowska-Wasiluk (2010). Previous descriptions of the fishes of the member have been restricted to material referring to Alopeidae and Cetorhinidae (Bieńkowska-Wasiluk & Radwanski 2009) as well as Gonostomatidae (Přikryl et al. 2012). New specimens of the fish fauna from this member are presented in this study, along with their paleoenvironmental, and paleogeographic implications.

Geological setting

The Dynów Marl Member is a marine sequence consisting of an alternation of bituminous, brown to light beige marlstones, brown and black cherts, shales and sandstones. It overlies bituminous black to brown cherts and shales of the Kotów Chert Member, and is overlain by bituminous brown to black shales and sandstones of the Rudawka Tractionite Member. The Dynów Marl Member occurs in most of the main tectonic units of the Outer Carpathians.
in Poland (see Kotlarczyk et al. 2006). The sediments of the Dynów Marl Member are rich in organic matter, barren of macrobenthos, but rich in fish.

The specimens were found in four different localities (Fig. 1A, B, electronic appendix 1). Three of them are in the Skole Nappe of the Outer Carpathians and are located near the villages of Futoma, Lubenia, and Wola Czudecka. The Jablonica Polska locality is in the Silesian Nappe. The Futoma (Błażowa) quarry is located 30 km southeast of Rzeszów city. The Lubenia and the Wola Czudecka localities are situated 20 km southwest of Rzeszów city (Bieńkowska-Wasiluk 2010). The Jabłonica Polska locality is 50 km south of Rzeszów city, and has two outcrops (Studencka et al. 2016). The Dynów Marl Member has a thickness ranging from 6 m in Jabłonica Polska to 30 m at Futoma locality.

The Dynów Marl Member is correlated with the nanoplankton zone NP23 of Martini (1971) and the ichthyofaunal zone IPM1 (Kotlarczyk et al. 2006), and is dated to the early Oligocene, ca. 32 Ma.

The deposits of the Dynów Marl Member document the environment of the northwestern part of the Carpathian Basin, and the northern Central Paratethys (Fig. 1C). The deposits accumulated in a variably deep basin with anoxic waters at and above the sea floor, with oxygenated deep waters, the activity of submarine fans, the activity of bottom currents, in some cases with debris flows and deposition from low-concentration turbidity currents as well as pelagic sedimentation and the blooms of coccolithophores (Krhovský 1981, Kotlarczyk et al. 2006, Bieńkowska-Wasiluk 2010, Górniak 2011, Kotlarczyk & Uchman 2012). Interpretations of the depositional system of the Menilite Formation, which comprises the Dynów Marl Member, are widely variable. Based on sedimentological analyses, paleontological analyses including foraminifera and fishes, alongside other considerations; deposition on the continental slope, submarine ridges and basin floor (e.g., Książkiewicz 1975, Olszewska 1985, Kotlarczyk et al. 2006, Szydło et al. 2014, Siemińska et al. 2020), and locally on the shelf is assumed (e.g., Olszewska
Based on sedimentological observations, Dziadzio (2018) has assumed a locally coastal environment. Jankowski (2015) has considered for some deposits (e.g., kliwa facies, diatomites) shelf environment, even with shallow sea setting.

The Dynów Marl Member is correlated with the Dynów Marlstone of the Menilitic Formation in the Central Paratethys (Czech Republic localities) and the Bituminous Marls in the southeastern Central Paratethys (Romanian localities) (see Krhovský et al. 1992, Baciu et al. 2016, Studencka et al. 2016). Sachsenhofer et al. (2017) has correlated this unit with the Polbian ('Ostracoda') Bed in the Eastern Paratethys (Russian localities, North Caucasus). The Dynów Marl Member is correlated herein with the Hochberg Member of the Bodenheim Formation (see Maxwell et al. 2016) in the Upper Rhine Graben (Western Paratethys) based on its nannoplankton record.

**Materials and methods**

The described material was collected from 1995 to 2018. The collection of fossil fishes at the Faculty of Geology, University of Warsaw comprises 67 specimens (some of them with counterparts, designated with ‘a–b’ in the collection numbers), and at the Muzeum Skamieniałości i Minerałów, Dubiecko, which comprises six specimens. The specimens were studied under a stereo microscope Nikon SMZ1000 at the Scanning Electron Microscope and Microanalysis Laboratory, Faculty of Geology, Warsaw University.

The sizes of the fishes were measured as standard length (SL), which is the length of a specimen measured from the anterior tip of the snout to the posterior margin of the hypurals.

**Systematic Paleontology**

Class Chondrichthyes Huxley, 1880
Subclass Euselachii Hay, 1902
Infraclass Elasmobranchii Bonaparte, 1838
Order Lamniformes Berg, 1958
Family Alopiidae Bonaparte, 1838

**Genus Alopias Rafinesque, 1810**

*Alopias aff. superciliosus* Lowe, 1841


**Description.** – The species is represented by four teeth of the lower jaw embedded in a marly matrix, exhibiting their labial view. A single tooth of the lower jaw, which is embedded in the marly matrix, is visible in lingual view. The teeth have a slender, acute and distally inclined cusp with a broad base. The mesial cutting edge is rather straight, whereas the distal one is concave, mainly at its base. Both cutting edges are sharp. The labial crown face is almost flat, whereas the lingual face is convex. Both faces are devoid of any ornamentation. The root has asymmetrical, well-separated and long lobes. The mesial lobe is longer than the distal one. The extremities of the lobes are rounded. The base of the crown extends laterally on the lobes by strong enameled shoulders. More details are available in Bieńkowska-Wasiluk & Radwanski (2009, as *Alopias* sp.).

**Remarks.** – The morphology of the examined specimens is consistent with that of *A. superciliosus* and matches perfectly with that of *A. aff. superciliosus* reported from the Oligocene (Cappetta et al. 2016). The specimens of *A. aff. superciliosus* from the Menilite Formation have been described by Bieńkowska-Wasiluk & Radwanski (2009) in Poland and Gregorová (2011) and Cappetta et al. (2016) in the Czech Republic.

**Ecology of related extant forms:** *Alopias superciliosus* (bigeye thresher shark) lives in coastal waters over the continental shelves, in the epipelagic zone far from the land; it is also caught near the bottom in deep water on the continental slopes, sometimes close to inshore in shallow waters. Its distribution in the water column ranges from 0 to 500 m, but it mostly cruises in depths below 100 m. It inhabits almost circumglobally tropical and warm temperate waters, where it feeds on pelagic fishes (Compagno 2002).

Family Cetorhinidae Gill, 1862

**Genus Keasius Welton, 2013**

*Keasius parvus* (Leriche, 1908)

**Figure 2B**

**Material.** – MWGUW ZI/57/101–102, ZI/57/141, ZI/57/142/1–3, Futoma; MWGUW ZI/57/140/a–b, Jablonica Polska; MWGUW ZI/57/010–012, ZI/57/204, Wola Czudecka.

**Description.** – The species is represented by ten complete and one fragmentary isolated gill rakers (branchiospines). Each gill raker has the shape of a narrow and elongated...
stick (filament) with a laterally flattened base, and reaches a length of up to 30 mm. The filament base is relatively narrow, moderately long, and strongly to moderately curved (terms follow Welton 2013). The medial process is triangular, moderately long and narrow. The bight is intermediate and ranges from subangular to rounded.

Remarks. – The morphology of the examined gill rakers is fully consistent with that of *K. parvus* reported by Welton (2013). The species is known from the Oligocene to the Middle Miocene, and in the past was usually described as *Cetorhinus* sp. or *C. parvus*. Welton (2013) assigned this species to the new genus *Keasius*. Detailed descriptions of specimens of *Keasius parvus* from the Menilite Formation have been given by Bieńkowska-Wasiluk & Radwaniski (2009, as *Cetorhinus* sp.) in Poland and by Gregorová (2011) and Cappetta *et al.* (2016) in the Czech Republic.

Ecology of related extant forms: The nearest relative to *Keasius parvus* is the recent *Cetorhinus maximus*. It is a coastal-pelagic and semi-oceanic filter feeder of boreal to warm-temperate waters (Compagno 2002). It occurs mainly in shallow coastal and epipelagic waters; its distribution in the water column ranges from 0 to 4000 m (Compagno 2002).

Order Squaliformes Goodrich, 1909
Family Centrophoridae Bleeker, 1859

**Centrophoridae gen. et sp. indet.**

*Figure 2C–E*

**Material.** – MWGUW ZI/57/139/a–b, Jablonica Polska.

**Description.** – The family is represented by a single tooth of the lower jaw. This tooth is labio-lingually compressed, blade-like, with a vertical basal groove on its lingual root, and with a broad cusp, which is directed distally. A distinct convex distal blade is present, which is separated from the principal cusp by a notch. The infundibulum is not preserved. There is no serration on the cusp and the blade, which indicates a juvenile individual (White *et al.* 2013).

Remarks. – The examined specimen shows a combination of diagnostic features typical of the *Centrophoridae* reported by White *et al.* (2013). The tooth is similar to *Centrophorus* and *Deania*.

Ecology of related extant forms: The extant *Centrophorus* is commonly found along the outer continental shelves and upper slopes, sustaining at 4000 m depth, but usually bottom-dwelling at depths between 200 and 800 m (Compagno *et al.* 2005). The extant *Deania* is commonly found either on or near the bottom, or well above it at the outer continental and insular shelves and upper slopes, in depths between 70 and 1790 m (Compagno 1984).

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Klein, 1885
Division Teleostei Müller, 1845
Order Clupeiformes Bleeker, 1859
Family Clupeidae Cuvier, 1817

**Clupeidae gen. et sp. indet.**

*Figure 3A*

**Material.** – MWGUW ZI/57/148–149, Jablonica Polska.

**Description.** – The family is represented by two cycloid scales, typical clupeid forms with transversal striae.

Remarks. – The scales described here match perfectly with those reported from the Oligocene by Szymczyk (1978) and those of recent fishes by Bräger & Moritz (2016).
Ecology of related extant forms: Clupeids are typically marine coastal, oceanodromous fishes; some enter brackish or fresh water. Their distribution in the water column mostly ranges between 0 and 200 m (Froese & Pauly 2021).

Order Argentiniformes Bertelsen, 1958
Family ?Argentinidae Bonaparte, 1846

Genus Glossanodon Guichenot, 1867

‘Glossanodon’ musceli (Paucă, 1929)

Figure 3B


Description. – The species is represented by nine complete and four incomplete skeletons. It is a small-sized fish (SL 42–54 mm) with an elongated, somewhat laterally compressed body. The small terminal mouth ends in front of the orbit; there are no teeth on the premaxilla and maxilla. The maxilla is slightly bent and has a flattened posterior projection, rounded antero-ventrally. There are 45–52 vertebrae, of which 25–29 are abdominal and 20–25 are caudal. The fins are without spines. A single dorsal fin with 10–13 soft rays is almost located above the midpoint of the body. The anal fin originates opposite and posterior to the dorsal fin (starts about four to eight vertebrae posterior to the last ray of the dorsal fin), and is composed of 12–13 (or slightly more) rays. The pectoral fin is situated near the ventrolateral part of the body flank and has 16–17 (or slightly more) rays. The pelvic fins originate beneath or slightly anterior to the dorsal fin. They are composed of about 10 rays. The caudal fin is deeply forked.
Remarks. – The specimens have the same morphology, diagnostic features and meristics as those of ‘$G$. musceli’ described by Jerzmańska (1967), Gregorová (2011), and Přikryl et al. (2016). The material described here shows the diagnostic characters (see Jerzmańska 1967), i.e., maxilla has a flattened posterior projection, rounded antero-ventrally, number of vertebrae, position of dorsal, anal, and pelvic fins, number of rays in pelvic fin. The species ‘$G$. musceli’ has been described by Paučă (1929, 1934), Daniltschenko (1960), Jerzmańska (1967), Přikryl (2013), and Přikryl et al. (2016). Jerzmańska (1967) claimed that it belongs to the Argentinidae. Prokofiev (2005a) erected a new genus Austromallotus in the family Osmeridae and ascribed the specimens from the Oligocene of the Caucasus to the species Austromallotus musceli. He suggested that the material described by Jerzmańska (1967) also belongs to A. musceli. Přikryl (2013) did not recognize A. musceli as a synonym of the species from the Carpathians. The important morphological features that can be used to discriminate between Argentinidae and Osmeridae are: (1) presence of a notch on the dorsal edge of the opercle; (2) strongly shortened and depressed neural spines on the anterior abdominal vertebrae; and (3) presence or absence of contact between the 1st and 2nd infraorbitals (Prokofiev 2005a). In the studied material, some specimens have strongly shortened and depressed neural spines on the anterior abdominal vertebrae, whereas others have elongated spines that are slightly inclined more posteriorly. The presence of the opercular notch and the arrangement of the 1st and 2nd infraorbitals cannot be verified because of the insufficient preservation of the investigated materials. Therefore, the traditional classification within the genus ‘Glossanodon’ is accepted here. More precise identification of the fishes from the studied area must wait until skeletons with preserved diagnostic characters are discovered.

Ecology of related extant forms: The recent Glossanodon occurs on the outer continental shelf and the upper slope, mostly near the bottom. Its distribution in the water column ranges between 70 and 1000 m (Froese & Pauly 2021).

Order Stomiiformes sensu Harold & Weitzman, 1996
Family Gonostomatidae Gill, 1893

Genus Scopeloides Wettstein, 1886

Scopeloides glarisianus (Agassiz, 1844)
Figure 3C


Description. – This species is represented by six complete and three incomplete skeletons. It is a medium-sized fish (SL 58–108 mm) with a moderately elongated body; both the head and the body are laterally compressed. The maximum depth of the body is 5.66.8 in SL. The orbit is small, the mouth is large and terminal, and the quadrato-joint with the mandible is clearly located posterior to the orbit. Teeth are present on the premaxilla, the maxilla, and the dentary. They are conical in shape and of two different lengths: Some are elongate and fang-like, with interspaces occupied by small needle-like teeth. There are 39–41 vertebrae, of which 18–19 are abdominal and 21–22 are caudal. There is a single dorsal fin with 14–15 soft rays, which is located above and slightly posterior to the midpoint of the body. The pectoral fin inserts close to the ventrolateral margin of the body flank and it has 11–12 rays. The anal fin inserts opposite and slightly posterior to the dorsal fin. It consists of about 25 rays. The pelvic fins are located in front of the dorsal fin, and have 8–9 rays. The caudal fin is deeply forked. One row of photophores (of the series PV, VAV, and AC) is poorly preserved close to the ventrolateral margin of the body flank.

Remarks. – The material described here shows the diagnostic characters of Scopeloides (see Prokofiev 2005b): frontalia with cancellate-cristate sculpture, number of vertebrae, number of rays in dorsal and anal fins, position of anal and pelvic fins, and anterior rays of the dorsal and anal fins distinctly larger than the posterior rays. The specimens have the same morphology and numbers of dorsal, pectoral and pelvic fin rays as those of S. glarisianus described by Gregorová (1997, 2011) and Grădianu et al. (2017). The number of vertebrae (3941) in the material is the same as that reported by Grădianu et al. (2017) and slightly greater as that given by Gregorová (1997, 2011; 38–39) and overlaps with data from Prokofiev (2005b; 37–40). The number of anal fin rays in the specimens described is smaller (25) than that reported by Gregorová (1997, 2011; 27) and Grădianu et al. (2017; 28–29), because of its insufficient state of preservation. Detailed descriptions of specimens of S. glarisianus from the Menilite Formation have been given by Gregorová (1997, 2011), Prokofiev (2005b), and Grădianu et al. (2017).

Ecology of related extant forms: The recent Gonostoma is mesopelagic and bathypelagic. Its distribution in the water column ranges between 50 and 1350 m, but mostly between 300 and 700 m by day and 50–200 m by night. It is found almost circumglobally in tropical and subtropical waters (Froese & Pauly 2021).
and between 50 and 500 m by night. It inhabits almost
but it is mostly found between 200 and 600 m by day

Vinciguerria obscura (Daniltshenko, 1946)

Figure 3D, E


Description. – This species is represented by seven complete and seven incomplete skeletons. It is a small-sized fish (SL 25–39 mm) with an elongated body; the head and the body are laterally compressed. The orbit is large. The mouth is large and terminal; the size of the teeth ranges from small to large (0.1–0.5 mm), but they are not highly elongate and fang-like. There are 39–43 vertebrae, of which 21–24 are abdominal and 17–19 are caudal. There is a single dorsal fin with slightly more than 10 soft rays, which is almost located above the midpoint of the body. The pectoral fin inserts near the ventrolateral margin of the body flank and has 10–11 rays. The anal fin has a moderately long base, and is located beneath and distinctly posterior to the dorsal fin. It is composed of slightly more than 15 rays. The pelvic fins insert anterior to the dorsal fin and have seven rays. The caudal fin is deeply forked. There are two ventrolateral rows of photophores on the body flank.

Remarks. – The combination of characters listed herein supports the attribution of the specimens to V. obscura (see Grădianu et al. 2020), including the position of the dorsal fin, and the maxilla bearing a series of small variably sized conical teeth. The examined specimens have the same morphology and similar meristics (number of vertebrae, and numbers of dorsal, anal, pelvic, and pectoral fin rays) as V. obscura, described in detail by Gregorová (2000, 2011), Prokofiev (2005b), and Grădianu et al. (2020).

Ecology of related extant forms: The recent Vinciguerria is mesopelagic and bathypelagic. Its distribution in the water column ranges from 50 to 5000 m, but it is mostly found between 200 and 600 m by day and between 50 and 500 m by night. It inhabits almost circumglobally tropical and subtropical waters (Froese & Pauly 2021).

Order Myctophiformes Regan, 1911
Family Myctophidae Gill, 1893

Genus Oligophus Gregorová, 2004

Oligophus moravicus (Paučă, 1931)

Figure 4A


Description. – This species is represented by five complete and three incomplete skeletons. It is a small-sized fish (SL 29–61 mm) with an elongated body; the head and the body are laterally compressed. The large terminal mouth ends far behind (about one eye diameter) a vertical line through the posterior margin of the orbit. The premaxillaries and dentaries show bands of densely spaced small teeth. There are 35–37 vertebrae, of which 14–16 are abdominal and 21–22 are caudal. Fin spines are absent. There is a single dorsal fin with 12–14 soft rays; its origin is slightly anterior to a vertical line through the mid-point of the body. The anal fin originates opposite to the posterior margin of the dorsal fin base. It has 13–16 rays. The pectoral fin is high on the body flank and has 11–13 rays. The pelvic fins insert beneath the origin of the dorsal fin and have eight rays. The caudal fin is deeply forked. Distinct groups of photophores (i.e., PLO, PVO, Prc, VO series, abbreviations follow Prokofiev 2006) are to be noticed on the body flank. The scales are cycloid with radial fissures.

Remarks. – The examined specimens show diagnostic features typical of Oligophus (see Gregorová 2004, Prokofiev 2006), including: long jaws, extending about one eye diameter behind a vertical line through the posterior margin of the orbit; number of vertebrae; presence of one photophore of PLO series at the level of the pectoral fin base; two photophores of PVO series below the pectoral fin base; presence of three photophores of Prc series near the caudal fin; presence of five photophores (VO series) behind the pelvic fins and anterior to the anal fin. The morphology and the osteology of the material described are the same, and the meristics is similar (number of vertebrae, and numbers of dorsal, anal, and pelvic fin rays) as O. moravicus, described by Gregorová (2004) and Prokofiev (2006). Otoliths of the species (previously under the name Diaphus longirostris) were described by Brzobohatý & Nolf (1995), Přikryl et al. (2017), and Brzobohatý & Bubík (2019).

Ecology of related extant forms: Myctophidae are very common and occur in all oceans, from Arctic to Antarctic waters. Many undertake diurnal vertical migrations, their distribution in the water column ranges from the surface to depths exceeding 2000 m. Many spend the night at depths between 30 and 100 m (Nafpaktitis 1984).

Order Gadiformes Goodrich, 1909, sensu Endo, 2002
Family Merlucciidae Gill, 1884
Genus *Palaeogadus* Rath, 1859

*Palaeogadus* sp.

Figure 4B

**Material.** – MWGUW ZI/57/138, Jablonica Polska.

**Description.** – This genus is represented by a single otolith, which is elongated and fusiform in outline. The size of this otolith exceeds 7 mm; otolith length to otolith height is about 2.2. Its ventral rim is shallow and smooth. The dorsal rim is gently curved. The sulcus is located in the middle of the long axis of the otolith. The oval ostium is smaller than the oval cauda. The pseudocolliculum is absent. The otolith resembles those of *P. germanus* and *P. rarus* (see Bratishko & Udovichenko 2013), both of which are known from otoliths and well-preserved skeletons from the Caucasus (Fedotov 1980). Unfortunately, the preservation of the present specimen does not allow assignment to a particular species.

**Remarks.** – The morphology of the examined otolith is similar to the otoliths of *Palaeogadus* reported by Bratishko & Udovichenko (2013) and Brzobohatý & Bubík (2019). The single otolith of *Palaeogadus* from the Dynów Marlstone of the Czech Republic has been described by Brzobohatý & Bubík (2019).

Ecology of related extant forms: *Merlucciidae* inhabit the continental shelf and upper slope, but some also enter estuaries and/or very deep waters, exceeding 1000 m (Cohen et al. 1990).

Order *Scombriformes* Rafinesque, 1810

Family *Euzaphlegidae* Daniltshenko, 1960

Genus *Palimphyes* Agassiz, 1844

*Palimphyes* sp.

Figure 4C

**Material.** – MWGUW ZI/57/157/a–b, ZI/57/158/a–b, MSMD Ma–47, Ma–113, Futoma.

**Description.** – This species is represented by three complete and one incomplete skeleton. It is a medium-sized fish (SL 55–140 mm) with an elongated and fusiform body, which is moderately compressed laterally. The mouth is moderately large and located terminally. The teeth on the premaxilla and the dentary are moderately strong. There are 36–37 vertebrae, of which 15–16 are abdominal and 21 are caudal. There are two dorsal fins, of which the first is short and separated from the second by about four rayless pterygiophores. The first dorsal has eight or nine spines, the second has about 20 rays. The anal fin has more than 14 rays. The pectoral fin inserts high on the body flank and has about 10 rays. The pelvic fins are located beneath and slightly posterior to the latter. They have about five rays. The caudal fin is deeply forked. The scales are ctenoid.

**Remarks.** – The total number of rays of the anal fin was unclear in the investigated material, because of its insufficient state of preservation. About 14 rays were observed, but it is probable that there were originally more. The described specimens show diagnostic features typical of *Palimphyes* (see Monsch & Bannikov 2012), including number of vertebrae, dorsal fins not closely adjoined, separated by rayless pterygiophores. The meristic data (number of dorsal, anal, pelvic and pectoral fin rays) of the examined specimens are similar to those of *Palimphyes*, described by Gregorová (2011) and Monsch & Bannikov (2012). The genus has been described in the Dynów Marlstone of the Czech Republic by Gregorová (2011).

Ecology of related extant forms: *Palimphyes* is an extinct genus of primitive scombriform fishes. Scombriforms are pelagic and marine (Carpenter et al. 1995, Collette et al. 2001). Their distribution in the water column ranges from 0 to more than 1000 (Froese & Pauly 2021).

Family *Trichiuridae* Rafinesque, 1810

Genus *Anenchelum* Blainville, 1818

*Anenchelum glarisianum* Blainville, 1818

Figure 4D

**Material.** – MWGUW ZI/57/125, MSMD Ma-2/L, Ma-3, Ma-4/L, Ma-10, Futoma.

**Description.** – This species is represented by three complete and two incomplete skeletons. It is a predominantly large fish, up to about 1350 mm SL (Gregorová, 2010). The materials that were investigated herein had an SL of 300 to about 1200 mm. The body is ribbon-like and remarkably elongate and laterally compressed. The mouth is large and terminal, the teeth are strong and usually fang-like in the anterior portions of the upper and lower jaws. The lower jaw articulation facet is located beneath the middle of the orbit or posterior to the latter. There are 115–117 vertebrae, of which 35–40 are abdominal and 77–82 are caudal. There is a single dorsal fin, which extends almost along the complete length of the body. It has more than 89 rays. There are spines in the anterior part of the fin, which are shorter than the soft rays of the posterior part of the fin. The anal fin has more than 56 rays. The pectoral fins are large and have more than...
10 rays, which insert close to the ventral margins of the body flanks. The pelvic fins are reduced to one flattened spine. The caudal fin is small and forked. Scales are absent.

Remarks. – In the examined material the total number of spines and soft rays of the anal and the dorsal fin is not completely clear, because of the insufficient state of preservation. The number of the pterygiophores of the dorsal fin’s soft rays slightly exceeds the number of adjacent caudal vertebrae. Two or three pterygiophores are supernumerary, and situated in the interneural spaces in the middle part of the body. Each of these additional pterygiophores is located between the neural spines of the 4th and the 6th, the 8th and the 12th or the 15th and the 18th caudal vertebrae. The investigated specimens have the main diagnostic character of *Anenchelum* (see Monsch & Bannikov 2012): pelvic fin reduced to only a single spine. They have typical characters of *Anenchelum*, including number of vertebrae, presence of a caudal fin, presence of supernumerary pterygiophores in the dorsal fin. The combination of characters listed herein supports the attribution of the specimens to *A. glarisianum* (see Monsch & Bannikov 2012), including: the total number of vertebrae, the number of abdominal and caudal vertebrae, and the lower jaw articulation facet’s location beneath the middle of the orbit. The morphology of the examined specimens is fully consistent with that of *A. glarisianum* reported by Gregorová (2010, 2011). Descriptions of specimens of *A. glarisianum* from the Menilite Formation have been given by Jerzmańska (1968), Gregorová (2010, 2011), Monsch & Bannikov (2012), and Přikryl (2013).

Ecology of related extant forms: Trichiurids live above the bottom of the continental shelf and slope worldwide (Parin & Nakamura 2002). Their habitats range from estuaries to open water up to 2000 m in depth (Gago 1998).
Discussion and conclusions

The fish assemblage from the Dynów Marl Member of the Menilite Formation in Poland described herein comprises three shark taxa and eight teleost taxa (Figs 2–4, electronic appendix 2). ‘Glossanodon’ musceli, Vinciguerra obscura, and Anenchelum glarisanum (electronic appendix 2) are for the first time reported in the Dynów Marl Member in Poland. Centrophoridae indet. is for the first time reported from the Menilite Formation. Most of the taxa have previously been reported from the Oligocene deposits of the Paratethys, but the assemblage of the Dynów Marl Member of Poland has not been analyzed in order to reconstruct the paleobiogeography and paleoenvironment. Consequently, this assemblage has the potential to provide such data in the northern Central Paratethys.

Paleobiogeography

Numerous authors have postulated an intermittent marine connection in the NP23 (about 30–32 Ma) between the North Sea, the Upper Rhine Graben, the Central and Eastern Paratethys (Carpathian Basin), and the Eastern Paratethys (Rögl 1999, Popov et al. 2002, Maxwell et al. 2016). A closure of marine seaways between the Paratethys and the World Ocean during the deposition of the Dynów Marl Member has been hypothesized by Studencka et al. (2016) and Sachsenhofer et al. (2017). Based on fossil fishes, the existence of a marine connection between the Upper Rhine Graben, the Central and Eastern Paratethys during the early Oligocene (28.5–34 Ma) and the Upper Rhine Graben has been interpreted as the Western Paratethys (Micklich & Parin 1996, Micklich 1998, Pharisat & Micklich 1998, Bannikov 2010).

Fish fauna from the Dynów Marl Member of Poland and the Dynów Marlstone of the Czech Republic is treated here as the Dynów Marl (DM) assemblage. It comprises 22 taxa of fishes, including three elasmobranch species and 19 teleost genera or species (Tab. 1). This assemblage is more similar to another assemblage of the Central Paratethys than to those of the Upper Rhine Graben and the Eastern Paratethys. The most similar fauna have been reported from Poland, the Czech Republic and Romania, containing more than 75% taxa of DM assemblage (77%, 82%, and 77%, respectively, Tab. 1). Other fauna with high levels of similarity to the DM fauna has been described from the North Caucasus of Russia (50%) in the Eastern Paratethys. The correlation between the DM fish assemblage and that of the Upper Rhine Graben is relatively low (41–45%), with nine shared taxa in France and ten in Germany. The connection between the Upper Rhine Graben and the Central Paratethys in NP23 is weakly supported by the occurrence of three fishes: the teleosts Anenchelum glarisanum and Auxides cernegurae, and the shark Keasius parvus. The presence of Alopias aff. superciliosus does not support such a connection, as this species seems to show a cosmopolitan distribution. The same genera can be found in both regions, such as Palaeogadus, Palaeorhynchus, and Palimphyes, but they exhibit a broad distribution in the Eocene–Oligocene. ‘Clupea’ and ‘Serranus’ should be revised to recognize their significance in paleobiogeographic considerations.

Anenchelum glarisanum has been reported from NP23 from the Dynów Marl Member of the Menilite Formation of Poland, the Marnes à Melettes of France (Pharisat 1991), the Dynów Marlstone of the Czech Republic (Gregorová 2011), and the Bituminous Marls of Romania (Ciobanu 1977, Baciu et al. 2016). This species has also been identified in the Psheka Horizon of Abkhazia (Monsch & Bannikov 2012). This horizon has been correlated with NP21–22 by Sachsenhofer et al. (2017). The species has been recognized in the Rupelian of the Glarner Schiefer of Switzerland and the Menilite Formation of Ukraine (Monsch & Bannikov 2012). The stratigraphic occurrence of the species is restricted to the Rupelian (electronic appendix 3).

Anenchelum glarisanum has furthermore been reported from Grube Unterfeld (Frauenweiler) locality in Germany (Micklich & Hildebrandt 2010, Monsch & Micklich 2018). The sediments of this locality belong to the Hochberg Member or the Bodenheim Formation (Maxwell et al. 2016). Referring to the materials of the Grube Unterfeld (“Frauenweiler”) locality in Baden-Württemberg (S. Germany), Monsch & Micklich (2018) have considered all specimens that have previously been assigned to A. glarisanum either as representatives of two undescribed new species of Anenchelum or as Anenchelum sp.

Keasius parvus is known from NP23 from the Marnes à Melettes of France (Pharisat 1991), the Hochberg Member of the Bodenheim Formation of Germany (Maxwell et al. 2016), the Dynów Marl Member of Poland, the Dynów Marlstone of the Czech Republic (Cappetta et al. 2016), and the Bituminous Marls of Romania (Baciu et al. 2016). The species has furthermore been reported from the Rupelian of the Glarner Schiefer of Switzerland (Welton 2013), the Azley Formation of Mainz Basin in Germany, and the Boom Clay Formation of the southern part of the North Sea Basin in Belgium (Reinecke et al. 2001, Cappetta et al. 2016).

Auxides cernegurae has been reported from the Hochberg Member of Bodenheim Formation (Maxwell et al. 2016) and Grube Unterfeld locality (Monsch & Micklich 2018), with sediments of the same formation of Germany, the Bituminous Marls of Romania and the lower part of the Menilite Formation of Ukraine (Monsch & Bannikov 2010).
Figure 5. Paleobathymetric analysis: bathymetric ranges of elasmobranch and teleostean taxa in the Dynów Marl Member (Outer Carpathians, Poland) and the Dynów Marlstone (Outer Carpathians, Czech Republic), and results of all the taxa and the benthic–benthopelagic taxa. Taxa names in black – taxa described in this study; taxa names in grey – taxa reported in previous publications by Cappetta et al. (2016), Gregorová (2011), Kotlarczyk et al. (2006), and Přikryl & Carnevale (2017, 2018). Dotted lines indicate the distribution of mesopelagic taxa at night, those distributions are not considered.
Table 1. Distribution of the genera and species identified in the Dynów Marls: the Dynów Marl Member (Outer Carpathians, Poland) and the Dynów Marlstone (Outer Carpathians, the Czech Republic) in other regions in the lower Oligocene. Abbreviations: x – presence in NP23; R – presence in the Rupelian; xR – presence in NP23 and other periods of the Rupelian (Jonet 1958; Jerzmańska 1968; Ciobanu 1977; Pharisat 1991; Pharisat & Micklich 1998; Constantin 1999; Brzobohaty & Nolf 1995; Reinecke et al. 2001; Prokofiev 2005b, 2006; Kottlarczyk et al. 2006; Bannikov 2010; Micklich & Hildebrandt 2010; Gregorová 2011; Monsch & Bannikov 2012; Príkryl et al. 2012, 2017; Welton 2013; Baciu et al. 2016; Cappetta et al. 2016; Maxwell et al. 2016; Gradianu et al. 2017; Príkryl & Carnevale 2017, 2018; Bordeiana et al. 2018; Brzobohatý & Bubík 2019).

<table>
<thead>
<tr>
<th>taxa, Dynów Marls: Dynów Marl Member and Dynów Marlstone</th>
<th>Switzerland</th>
<th>France</th>
<th>Germany</th>
<th>Germany</th>
<th>Belgium</th>
<th>Poland</th>
<th>this study</th>
<th>Poland</th>
<th>Czech Republic</th>
<th>Ukraine</th>
<th>Romania</th>
<th>Russia North Caucasus</th>
<th>Abkhazia</th>
<th>Azerbijan</th>
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<tr>
<td></td>
<td>north-western Tethys</td>
<td>Upper Rhine Graben</td>
<td>North Sea</td>
<td>Central Paratethys</td>
<td>Eastern Paratethys</td>
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<tr>
<td><em>Keasius parvus</em></td>
<td>R</td>
<td>x</td>
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<td>R</td>
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<td>x</td>
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<tr>
<td><em>Squalus cf. alsaticus</em></td>
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<td><em>Alopias aff. superciliosus</em></td>
<td>R</td>
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<td>‘Clupea’</td>
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<td>‘Clupea sardinates’</td>
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<td>‘Glossanodon’ musculi</td>
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<td><em>Scopeloides glarisanus</em></td>
<td>R</td>
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<tr>
<td><em>Vinciguerria obscura</em></td>
<td>xR</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>R</td>
<td>xR</td>
<td>R</td>
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<tr>
<td><em>Oligophus moravicus</em></td>
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<td>xR</td>
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<td>‘Serranus’</td>
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<td><em>Gephyroberyx</em> cf. <em>darwinii</em></td>
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<td><em>Zenopsis clarus</em></td>
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<tr>
<td><em>Palaeogadus</em></td>
<td>R</td>
<td>x</td>
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<td>x</td>
<td>xR</td>
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<tr>
<td><em>Palimphyes</em></td>
<td>R</td>
<td>x</td>
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<tr>
<td><em>Anenchelum glarisanum</em></td>
<td>R</td>
<td>x</td>
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<td>xR</td>
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<td><em>Palaeorhynchus</em></td>
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<td><em>Scorpaenoides</em></td>
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<tr>
<td>‘Centriscus’ = <em>Aeoliscus</em></td>
<td>x</td>
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<tr>
<td>‘Brotula’ longipinnata</td>
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<td><em>Propteridium profundae</em></td>
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<tr>
<td><em>Louckaichthys novosadi</em></td>
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<tr>
<td><em>Scophthalmus stamatini</em></td>
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<tr>
<td>In common with Dynów Marls (number of taxa)</td>
<td>4</td>
<td>9</td>
<td>10</td>
<td>4</td>
<td>2</td>
<td>17</td>
<td>9</td>
<td>18</td>
<td>6</td>
<td>17</td>
<td>11</td>
<td>6</td>
<td>4</td>
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<tr>
<td>In common with Dynów Marls</td>
<td>23%</td>
<td>41%</td>
<td>45%</td>
<td>18%</td>
<td>9%</td>
<td>77%</td>
<td>41%</td>
<td>82%</td>
<td>27%</td>
<td>77%</td>
<td>50%</td>
<td>27%</td>
<td>18%</td>
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</table>
This species is also known from the Pshekha Horizon of Abkhazia and the North Caucasus in Russia (Monsch & Bannikov 2012).

Scopeloides glarisianus, Vinciguerria obscura, and Oligophus moravicus have been reported from the lower Oligocene zones NP21–23 of the Central and Eastern Paratethys. They have also been described from the Dynów Marl Member of Poland, the Dynów Marlstone of the Czech Republic (Gregorová 1988, 2011), the Kotów Chert Member of Poland (Kotlarczyk et al. 2006), the lower part of Menilite Formation of Ukraine (Prokofiev 2005b, 2006), the Bituminous Marls of Romania (Ciobanu 2005b, 2006), the Kotów Chert Member of Poland (Kotlarczyk et al. 2006), the Rupelian Glarner Schiefer of Switzerland and the Boom Clay Formation of the Central (Carpathian Basin). The close relative of this species, the shark Alopias aff. superciliosus is known from NP23 from the Dynów Marlstone of Czech Republic (Cappetta et al. 2016). The species has been reported from the Rupelian of the Azley Formation of the Mainz Basin in Germany and the Boom Clay Formation of the southern part of the North Sea Basin in Belgium (Reinecke et al. 2001, Cappetta et al. 2016).

The distribution of Anencelum glarisianum, Auxides cernegurae, Keasius parvus, Scopeloides glarisianus, Vinciguerria obscura, and Oligophus moravicus (Tab. 1) confirms a marine connection during the Rupelian between the North Sea, the northwestern Tethys, and the Central (Carpathian Basin) and Eastern Paratethys. The occurrence of the shark K. parvus supports a marine connection during the Rupelian between the North Sea, the Upper Rhine Graben and the Central Paratethys (Carpathian Basin). The close relative of this species, the recent Cetorhinus, is cosmopolitan. Therefore, further research is necessary to assess the significance of this species.

Paleoenvironment

The composition of the ichthyofauna is herein used to evaluate the paleobathymetric range, via a comparison with the depth range of related extant taxa, according to the methods described and discussed by Nolf & Brzbohaty (1994) and Lin et al. (2016). The paleobathymetric method is based on the analysis of taxa reported here and previously in the Dynów Marl Member in Poland and in the Dynów Marlstone in the Czech Republic. Corresponding information concerning the applicable extant taxa has already been given in the preceding text (Systematic Paleontology – Ecology of related extant forms), and for taxa reported previously and not described here, information has been taken from Cappetta et al. (2016), Froese & Pauly (2021), Greenfield et al. (2008), Kotlarczyk et al. 2006, and Møller et al. (2016). For the results, the analysis and the associated diagrams, see Fig. 5. For some of the Dynów Marls taxa it is, however, not possible to state which species are related to the fossil taxa, and so the depth distribution of all extant species of the same genus or family has been taken into account.

The ichthyfaunal assemblage of the Dynów Marl Member and the Dynów Marlstone contains the highest percentage (78–87%) of fishes in the depth interval between 0 and 500 m (Fig. 5). The assemblage of benthic and benthopelagic fishes contains the highest percentage (71–93%) in the same interval. The benthic and benthopelagic taxa are more important for the bathymetric interpretation (Lin et al. 2016).

Consequently, it can be concluded that the fish assemblage of the Dynów Marls predominantly lived in the depth interval between the sea level and a depth of about 500 m, confirming the variable depths of the basin, including a deep-water as well as a shallow sea environment that prevailed during the deposition of the Dynów Marl Member and the Dynów Marlstone of the Menilitic Formation in the northern Central Paratethys.

This conclusion is consistent with the analysis by Cappetta et al. (2016) of the shark assemblage of the Menilitic Formation in the Czech Republic. This assemblage contains 78–89% of fishes in the depth interval between 0 and 500 m. The ichthyofauna of the Upper Rhine Graben contains more than 80% of fishes in the depth interval between 0 and 50 m, about 50–60% in the depth interval between 50 and 200 m, and less than 20% in the depth interval between 400 and 800 m, indicating distinctly shallower waters (Maxwell et al. 2016). The absence of deep-water taxa like Scopeloides glarisianus, Vinciguerria obscura, and Oligophus moravicus in the Upper Rhine Graben (Western Paratethys) corresponds well to a moderately shallow environment. The absence of these fishes in the Polbian Bed in the Eastern Paratethys (Russian localities, North Caucasus) may result from the absence of sufficiently deep zones in the basin.

The bathymetric distribution of fishes of the Dynów Marls supports the presence of oxygenated epipelagic and mesopelagic zones, as well as sublittoral and upper bathyal zones in the northern Central Paratethys. However, an unbioturbated, mostly dark-brown sediment that contains well-preserved skeletons of fishes is indicative of anoxic waters at and above the sea floor (Fig. 6). This is supported by the limited presence of typical demersal fishes and the paucity of benthic fauna. Therefore, considering the presence of anoxic waters, the basin was likely deeper than 500 m.
The low-diversity-specific bivalve assemblages, a specific ostracod association, and a nearly monotypic calcareous nannoplankton flora from the Paratethys during the middle Rupelian suggest reduced salinity, estimated between 12 and 15‰ (Rusu 1988, Popov et al. 2002, Melinte-Dobrinescu & Bruster 2008, Studencka et al. 2016). During the deposition of the Dynów Marl Member brackish conditions have been hypothesized (Studencka et al. 2016).

According to the life habits of individuals of extant comparative species, the Dynów Marl Member bears a typical marine ichthyofauna. Typical brackish fishes have not been recovered, and euryhaline fishes may only be represented by some species of Bythitidae, Clupeidae, Merlucciidae, Ophidiidae, Trichiuridae, and Scophthalmus. Kotlarczyk et al. (2006) have reported freshwater Barbus, based on the presence of a single scale. Most previous records of freshwater fishes in the Oligocene of the Carpathians after revision have not been confirmed (e.g., Jerzmańska 1968, Constantin 1999). This record is not listed in paleobathymetric analyses and palebiogeographic considerations, because in needs to be reviewed or supported by the presence of additional specimens. Extant representatives of the families Go­nostomatidae, Phosichthyidae, and Myctophidae, are typical of a fully marine environment, where they inhabit the deep pelagic zones (shared depth range between 300 and 600 m). Records that can be assigned to these families constitute a significant part of the fish assemblage described in this paper (42%, Fig. 7). Therefore, normal salinity can be inferred for the upper part of the mesopelagic zone during the deposition of the Dynów Marl Member.

Brackish conditions can be hypothesized locally (based on bivalve, ostracod and nannoplankton assemblages), near the freshwater influx or in surface waters and shallow-marine benthic waters.

### Stratigraphic significance

The ichthyofaunal zone IPM1 of the Carpathian Oligocene was correlated with the assemblage of the Pshekha Horizon in the Eastern Paratethys by Jerzmańska & Kotlarczyk (1983). Based on the occurrence of Aeoliscus, Vinciguerra obscura, Oligophus moravicus, and Scope­loides glarisanus, the Carpathian ichthyofaunal zone IPM1 has been regarded by Prokofiev (2007) as contemporaneous with the upper Pshekian stage of the Eastern Paratethys. In the Carpathians (Central Paratethys), the IPM1 zone has been correlated with the Kotów Chert Member and the Dynów Marl Member (Kotlarczyk et al. 2006). Therefore, the present ichthyofauna supports a correlation between the upper Pshekian stage of the Eastern Paratethys and the Dynów Marl Member of the Central Paratethys. By contrast, many authors correlate the early Solenovian (Polbian) stage of the Eastern Paratethys with the Dynów Marl Member (Studencka et al. 2016; Sachsenhofer et al. 2017, 2018). Prokofiev (2007) has correlated the early Solenovian with IPM 2. This correlation is affected by a distinctly reduced number of fishes in the early Solenovian in comparison to the upper Pshekian. This scarcity of fishes may result from significant changes in the environment of the Eastern Paratethys, specifically decreased salinity and the shallowing of the sea. Therefore, it is concluded here that particular ichthyofauna of the Dynów Marl Member links this unit with the upper Pshekian stage of the Eastern Paratethys. The deviations between the assemblages of the Dynów Marl Member and the early Solenovian probably
owe to considerable paleoenvironmental differences between the Central and the Eastern Paratethys.

Based on the occurrence of Vinciguerria obscura, Oligophus moravicus, and Scopeloides glarissianus, a correlation among the Dynów Marl Member of Poland, the Dynów Marlstone of the Czech Republic, the lower part of the Menilite Formation of Ukraine, and the Bituminous Marls of Romania is confirmed.

Acknowledgments

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**Electronic Appendix**

Appendix 1. Studied specimens from the Outer Carpathians and its localities.

Appendix 2. List of fish fauna of the Dynów Marl Member of the Menilite Formation in Poland.