

A FRAMEWORK OF ICHTHYOFAUNAL ECOSTRATIGRAPHY OF THE OLIGOCENE–EARLY MIOCENE STRATA OF THE POLISH OUTER CARPATHIAN BASIN

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Abstract: The paper presents the results of an analysis of ichthyofaunal variability throughout the section of the Menilite-Krosno Series (MKS) in the Outer Carpathians of Poland. The studied tanathocoenoses were formed at the bottom of a more than 2,000 m deep northern basin of the Tethys, being largely represented by the continental rise and bottoms of its narrow furrows, and – to a lesser degree – the continental slope and slopes of a submarine high. Lateral variability of statistically representative assemblages of tanathocoenoses hosted in thin, isochronous horizons is interpreted as a result of both local changes of ichthyocoenoses and the influence of post-mortem relocation of fishes that mainly dwelled the shelf and upper continental slope. Vertical variability, in turn, is considered as a resulting from changeable conditions of the ecological environment, the input and outflow of taxa whose evolution proceeded in the Indo-Pacific area, and the species extinction.

Changeability of ichthyofauna within a ca. 16-m.y.-long interval made it possible to document and formally describe 9 zones and 4 subzones of ichthyofauna of ecostratigraphic character. These zones comprise index, representative and accompanying taxa that belong to different ecological groups. Conceptual models of the origin of ichthyofaunal assemblages of individual zones are presented. It is suggested that the origin of assemblage differentiation resulted from the appearance and disappearance of the oxygen minimum zone in the water column, global and local sea level changes, topography of the basin bottom, as well as final basin infilling by sediments of submarine fans.

The described and preserved collection of fossil Carpathian fishes, housed at the Department of Palaeozoology of the University of Wrocław, requires further specialized palaeontological studies in order to reconstruct a more complete composition of the Oligocene–Early Miocene ichthyofauna.

Key words: fossil fish collection, Teleostei, deep-sea sediments, lithostratigraphy, biostratigraphy, fish eco-assemblages, models of changes, ichthyofaunal zonation, ecostratigraphy, Oligocene, Early Miocene, Outer Carpathians, Poland.

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INTRODUCTION: A REVIEW OF PALAEOICHTHYOLOGICAL STUDIES IN THE POLISH CARPATHIANS

Modern, large-scale studies of the Palaeogene and Neogene ichthyofauna of the Polish Carpathians were initiated at the turn of the 1950s by a palaeozoologist, Anna Jerzmańska (Jerzmańska, 1958, 1960), who in the successive years closely cooperated with Carpathian geologists, S. Jucha (Jerzmańska & Jucha, 1963) and J. Kotlarczyk (see references). During the 35-years-long studies, the research team included as well A. Jerzmańska's disciples, palaeozoologists Wiesława Szymczyk and Jacek Świdnicki, and – starting from 1972 – Ewa Świdnicka. Fish exploitation was also aided by helpful participation of family members of

principal investigators, namely: Assoc. Prof. Jerzy Jerzmański, geologist, Jan and Ewa Jerzmański, Ewa Sztolcman-Kotlarczyk, as well as friends, like Franciszek Ryzner, botanist, and students of the University of Wrocław. Independent studies of the Carpathian ichthyofauna were carried out by Dr. Teresa Śmigielska (Śmigielska, 1962).

A close cooperation between palaeozoologists and geologists brought about important progress in research into the Carpathian ichthyofauna. It was quickly found out that the section of the Menilite Formation, abundant in fossil fish, bears a succession of three, superimposed one upon an-

other, clearly different ecological assemblages of ichthyofauna which were provisionally named as the lower bathy-pelagic, neritic-sublittoral, and upper bathy-pelagic ones (Jerzmańska & Kotlarczyk, 1968; Kotlarczyk & Jerzmańska, 1976); instead of previously described, chronologically unordered, mixed assemblages composed of both shallow and deep-water fish.

It was also documented that the characteristic assemblage of bathy-pelagic fish, described from the shaly Jasło Limestones forming intercalations within the Krosno Formation at Sobniów near Jasło (Jerzmańska, 1960), is repeated in an exposure situated some 50 km away, at Łubno near Dynów, although within shales of the Menilite Formation (Jerzmańska & Jucha, 1963). This finding led to a conclusion that ichthyofauna of the Outer Carpathians could be used for stratigraphic purposes, and confirmed a concept of facies interchanging between the two mentioned formations (Jucha & Kotlarczyk, 1958, 1959; Shakin, 1958; Koszarski & Żytko, 1961). The latter provided a basis for distinguishing the Menilite-Krosno Series (Jucha & Kotlarczyk, 1961). Both lithofacies of this series were deposited at the same time in the Outer Carpathian flysch basin, namely between the onset of the Oligocene (and in the southern part probably from the Priabonian) through the mid-Burdigalian. The last episode of deposition is represented in the Menilite lithofacies by the Leszczawka Diatomite Horizon (Kotlarczyk, 1966).

The first summary of palaeontological studies of fish comprised in the Menilite beds, based on some 2,000 specimens collected at a dozen or so exposures, was published in the Dr. Sc. thesis by A. Jerzmańska in 1968.

The following 25 years witnessed further intensive, systematic exploration of ca.150 exposures situated in the Outer Carpathians east of the Wisłoka River. Field studies resulted in collecting nearly 13,000 fish specimens which were described by A. Jerzmańska usually up to the genus (ca. 7,600 specimens), rarely species (ca. 3,100 specimens), and sometimes only family (ca. 1,100 specimens) or order (ca. 400 specimens) levels. It should be mentioned in this place that determination up to the genus level is sufficient for drawing ecological and ecostratigraphic conclusions (Jerzmańska & Kotlarczyk, 1988; Gregorová, 1997).

A minor part of this collection, numbering ca. 4,000 specimens, was described in publications and catalogued, while the remaining 9,000 specimens was accompanied by field labels only and required detailed inventory.

Elaboration of this data set included different approaches. The main emphasis was put on palaeontological identification of preserved skeletons, including the description of new taxa (5 genera and 9 species), as well as verification of some earlier-distinguished taxa (cf., for instance, Jerzmańska, 1967a, 1968, 1974, 1979; Świdnicki, 1986, 1988a; Tyler *et al.*, 1993).

Another approach consisted in looking for detailed variability of fish assemblages in the log of the Menilite-Krosno Series. These studies resulted in identification of six ichthyofaunal zones of Oligocene (Kotlarczyk & Jerzmańska, 1976) and one of Early Miocene ages (Jerzmańska & Kotlarczyk, 1981, 1988). These zones are of ecostratigraphic character; they also comprise a component associated with

evolutionary changes of Teleostei (Jerzmańska & Kotlarczyk, 1981). Apart from bone fragments, the studies concentrated on the variability of fish scales of some common genera (Szymczyk, 1978) in the entire section of the Menilite-Krosno Series, as well as on occasionally occurring crab ichthyofauna (Jerzmańska, 1967b) and fragments of brown seaweeds. A spectacular finding was identification in Zone 6 of a specific assemblage of deep-water fish, pipefish, and air bladder-bearing algae, what justified calling this assemblage a quasi-sargassum one (Jerzmańska & Kotlarczyk, 1975, 1976), predating the recent sargassum assemblage.

The third approach included an analysis of lateral extent of the distinguished zones and an attempt at showing correlation possibilities of different sections of Menilite beds exposed at different sites and situated in different tectonic units throughout the Carpathian arc (Kotlarczyk & Jerzmańska, 1980). This attempt was also applied, basing on published data pertaining to fish assemblages, to the Palaeogene and Neogene sequences of the Caucasus (Jerzmańska & Kotlarczyk, 1983), and – later – the Alpine Foredeep and Rhine Graben (Kotlarczyk & Jerzmańska, 1988a).

Occasionally, attempts were made at determining the range of variability of fish assemblages within stratigraphic logs and between individual sites (Jerzmańska *et al.*, 1973; Kotlarczyk *et al.*, 1975), and at explaining the nature of this variability (Jerzmańska & Kotlarczyk, 1973, 1979; Jerzmańska & Kotlarczyk, 1991).

Due to a number of reasons, no currently-made full lithological documentation was performed at every explored site. Detailed lithological-sedimentological logs were compiled for some more important sites only, like those at Jamna Dolna (Jerzmańska & Kotlarczyk, 1968) or Bachów (Jerzmańska & Kotlarczyk, 1975). For some of the exposures, only rough sketches were drawn showing the position of fish-bearing layers within distinguished lithological complexes. In most cases, the reason for such an approach was the lack of clear taxonomic and ecological differentiation of fish assemblages among individual layers. At such exposures, particularly small ones, exploitation of fish in successive seasons was frequently carried out “without determining stratigraphic position” (wdsp) in the section, and the collected assemblage was treated as representing the entire bed sequence of the exposure.

The collected specimens were labelled in the field by the name and number of exposure and the layer's number or symbol. A complete inventory was only made for those specimens which were later described in publications.

In the end of the 1990s, therefore, a large regional collection of Palaeogene and Neogene fish, collected systematically and in such a way so as to make it possible to assign the majority of specimens (including the oldest representatives of many taxa) to the log of the Menilite-Krosno Series and individual time slices within the Early Oligocene–Early Miocene interval, did not possess full scientific value and could not be thoroughly interpreted.

The final systematic studies and geological documentation, combined with verification of the proposed ichthyofaunal zonation scheme based on the entire Carpathian collection, were originally planned for the second half of the

1990s. Unfortunately, prolonged illness of Prof. A. Jerzmańska made these plans unrealistic. In 2000 it became evident that final studies including Prof. Jerzmańska's participation could not be realised. Therefore, it was decided to continue the work by the remaining members of the team and a few invited collaborators. We also accepted that the names of taxa either introduced or accepted by Prof. Jerzmańska in papers by her disciples, should remain unchanged. It was not our intention to emendate the name of taxa without Prof. Jerzmańska's approval. The extent and direction of these possible changes are referred to in respective paragraphs of the text. This approach will enable for showing the state of recognition of the collection at the level achieved by this untiring researcher of fossil ichthyofauna.

Aim of study

To achieve the principal aim of this study, mentioned in its title, it was necessary to realize several tasks, including:

1. compilation of an integrated computer catalogue of all specimens of the collection, including their affiliation to the respective exposures and layers;
2. geological-lithological documentation of ichthyofauna-bearing exposures;
3. constraining the temporal array of exposures within: partial stratigraphic sections, complete synthetic sections of individual formations (constructed for closely-spaced sections), and composite sections, characteristic of larger zones (areas) composed of several synthetic sections;
4. description of taxonomic composition of specimens comprising the collection, using the current systematic subdivision;
5. reconstructing palaeoecology of fish assemblages within the distinguished ichthyofaunal zones, basing on literature data pertaining to palaeoecology of relevant families and genera.

The above data provided solution to the following final tasks, namely:

6. verification of the earlier distinguished ichthyofaunal zones, including attempts at their supplementing;
7. elaboration of a new standard of ecostratigraphic subdivision of the Menilite-Krosno Series in the Polish Carpathians, based on ichthyofauna;
8. elaboration of a scheme of ecological changes in the Polish segment of the Tethyan basin during 17–34 Ma interval;
9. deciphering the origin of variability of ichthyofaunal assemblages.

The following people took place in realisation of individual tasks:

Re. 1. Ewa Świdnicka (chairman), Krzysztof Stefaniak, Paweł Socha;

Re. 2. Janusz Kotlarczyk (chairman), Tadeusz Leśniak, Andrzej Joniec, Małgorzata Bienkowska, E. Świdnicka;

Re. 3. J. Kotlarczyk, accompanied by T. Leśniak, A. Joniec, and M. Bienkowska;

Re. 4. E. Świdnicka;

Re. 5. Teresa Wiszniowska, accompanied by K. Stefaniak;

Re. 6–9. J. Kotlarczyk.

General supervision was taken care of by Janusz Kotlarczyk.

Research into Oligocene–Miocene fish: a state-of-the-art

Older, i.e. pre-dating the 1960s, collections of Palaeogene and Neogene fish from the Moravian, Polish, Ukrainian and Romanian Carpathians, Switzerland, France, Germany, Hungary, Italy, and California (see, for instance, Cosmovici, 1887; Simionescu, 1905; Rychlicki, 1909; Arambourg, 1925; Leriche, 1927; Erasmo, 1930; Paucă, 1933; Weiler, 1933; Theobald, 1934; David, 1943; Kalabis, 1948; Horbatsh, 1956;) are poorer in the number of specimens, were usually assembled without applying stratonomic methods, and can be used – after necessary verification – in an analysis of the age of appearance of individual taxa of Teleostei, their palaeozoogeography, and – first of all – in osteological and phylogenetic studies. In some cases, collection descriptions took only into account ecological questions and the importance of fish for palaeobathymetric reconstructions (e.g., Arambourg, 1927, 1929; Paucă, 1933; David, 1957). Only more recent collections of fossil fish, collected mainly from the Upper Miocene strata of the Mediterranean (Tethys) were thoroughly investigated (Gaudant, 1978, 1989; Bradley & Landini, 1984; Bedini *et al.*, 1986). Such studies included stratigraphic position of fish-bearing layers in sedimentary sequences, bathymetric and ecological aspects, as well as modelling of formation of particular fish assemblages. However, these collections are not very rich, usually numbering ca. 100 specimens per section, poor in taxa, and derived from either solitary layers or thin packets of sediments, representing a narrow time interval. They cannot, therefore, serve as a basis for tracing changes in the Tethyan ichthyofauna in a longer period of time. Of comparable importance is the collection from Froidfontaine (Pharisat, 1991), restricted to a portion of the Rupelian, although very rich in specimens (ca. 12,000 specimens, including more than 5,000 of *Clupea sardinites*, 5,000 of *Aeoliscus heinrichi*, and 1,300 of *Cethorinus parvus*).

Collections derived from the Romanian Carpathians and Caucasus (Russia, Osetia, Azarbaijan), although comparable as to the age and number of specimens, are in many aspects inferior to the Polish collection. The Romanian collections (the older one housed in Bucharest, the younger ones derived from Piatra Neamt; e.g., Ciobanu, 1977 or Homoriciu-Jonet, 1958) were usually assembled by different investigators who seldom paid attention to detailed stratigraphic position and sedimentological context. These collections require thorough taxonomical revision. The most complete and best described Caucasian collections, in turn, represent sets of data of differentiated value. They were assembled by different authors in different times, at broadly-spaced, distant sites. Moreover, these authors applied different lithostratigraphic subdivisions to the fish-bearing strata of the Khadum and Maikop beds (cf. Danilchenko, 1960, 1980). The stratigraphic position of some of these collections is not certain, although a few of them were described using the stratonomic principles (e.g., Hecker & Merklin,

1946). The temporal and spatial distributions of these collections are, therefore, not reliable. That is why the recently published inventory of fish assemblages in question (Bannikov & Parin, 1997) applies very broad time intervals to individual taxa: (1) Early Oligocene, (2) Late Oligocene, (3) lower Early Miocene, and (4) upper Early and Middle Miocene. The main drawback of the Caucasian collections, however, is the lack of distinctly individualised bathypelagic assemblage in the upper Oligocene and lower Miocene strata. There usually prevail epipelagic and, in part, demersal assemblages. In other words, this ichthyofaunistically well described area is not typical of the northern Tethyan basin (cf. the presence of endemic fauna) and its changes which, in turn, are observed in the Carpathians.

New descriptions of a collection derived from the Moravian Carpathians (e.g., Kalabis & Schultz, 1974; Brzobohatý *et al.*, 1975), supplemented by findings of new sites (e.g., Gregorová, 1989, 1993, 1997) do not provide complete record of ichthyofaunal changes in the Oligocene–Early Miocene. The rich in fish Menilite Formation is here represented by Rupelian strata only, while the overlying Ždanice – Hustopeče strata, a facies of the Krosno Formation, Chattian–Aquitania (Egerian) in age, bear only three sites providing infrequent specimens.

The above review clearly shows that only the collection from the Polish Carpathians can help in thorough analysis of marine environments of the northern Tethyan basin in Oligocene–Early Miocene times. This worldwide unique collection was completed by one team of geologists and palaeozoologists using the stratonomic method in close relation to the local lithostratigraphy, and described by one of the most famous Polish palaeoichthyologists and her disciples.

It seems likely that only this collection can serve as a basis for establishing a standard of ichthyofaunal changes in the Oligocene–Early Miocene, necessary for future research and comparative studies of the Palaeogene–Neogene ichthyofauna.

METHODS

Realisation of the first three indirect goals required application of well-known routine methods.

1. Construction of a digital catalogue of the collection, CollFishCarpathZPALWr, including different assemblages distinguished according to the degree of taxa description (A, B, C, D, H, Ł, N, O_s, PB, R), required unification of the mode of archiving of all specimens. Each specimen was properly secured against destruction (glueing together, sometimes conservation), given inventory number, new label, and a set of archival and descriptive files, wrapped in string-tied plastic bags, and put into a properly labelled box. Boxes bearing classified specimens were stored in numbered chests of drawers, specially manufactured for this collection, and housed in a separate room of the Department of Palaeozoology.

Inventory work was associated with verification of specimens basing on analysis of different archival documents. For each specimen, its taxonomical documentation, both archival and published one, was assembled and its po-

sition in the relevant exposure was verified by confronting label description with archival documentation of the site.

Specimens derived from sets described in publications (A, B, H, Ł, O_s) or manuscripts (C) were given relevant bibliographic descriptions on the labels.

The entire data base was prepared with the help of MS ACCESS 2002 program. The data base is characterised by an unified record of information stored in three systematic catalogues, including: (1) taxa of fossil fish (alphabetical catalogue); (2) sites (alphabetical catalogue); and (3) fish specimens. These catalogues bear the following data: (1) number of specimen, (2) name of taxon, (3) name of the site, (4) specimen description, (5) accompanying taxon, (6) archival number, (7) place of storage, (8) taxonomical rank, and (9) bibliographic information.

2. Geological documentation of exposures was a long-lasting process. Out of 213 exposures from which fossil fish of the collection were assembled, only 28 were logged in detail in the years of 1965–1991. After commencement of this work and field inspection it turned out that 29 exposures, sampled at the incipient stage of ichthyofaunal investigation, could not be identified without participation of A. Jerzmańska, and that further 16 exposures could not be localised in the field. Moreover, it became evident that 23 exposures (including very important ones of the Jasło Limestones at Sobniów and Łubno-Łazek) had been either completely destroyed or dumped. Fortunately, from 2/3 of these 68 lost exposures only solitary specimens or not numerous (up to 10 specimens) fish assemblages were collected. Out of the remaining 117 exposures, already 42 supplied similarly insignificant number of specimens (35 exposures numbering 5 specimens each) of poorly informative composition. In addition, these exposures represented very short intervals of the stratigraphic section and that is why it was decided not to log them. Finally, 75 exposures were logged in detail.

The principal goals of logging were to reconstruct sedimentary environment of the studied strata, favourable for the formation of taphocoenoses in the analysed segments of a formation, as well as to correlate the exploited fish-bearing horizons with the record of depositional events.

Fish skeletons occur exclusively within pelitic sediments (claystones, siliceous-clayey or marly shales, laminated limestones, bedded marls) which are principal components of the Menilite Formation. Therefore, quick and unequivocal discrimination between the end members of the Bouma sequence and pelagic sediments and other clayey and silty depositional events raised certain difficulties. In such situations, traditional way of notation (e.g., Ghibaudo, 1992) was replaced by lithological description. Experience gathered during many years of study had already helped to decide that, for instance, sheet-like shales represented sediments of frequently recurring diluted turbidity currents, and that shales of sliver-like fissility were in fact clayey unifites. Such a form of lithological description was also applied to the previously-performed logging of 28 exposures, in order to maintain this way of notation. In many cases, recurrent logging was impossible due to destruction of exposures.

Analysis of large exposures required their graphic representation at a scale smaller than 1:20, resulting in syn-

thetic and generalised pictures. Lithological sections bear data pertaining to CaCO₃ and silt contents, presence of isolated ripplemarks, and secondary silification of sediment. A set of sections of 103 exposures makes up geological-factographic part of the collection. Apart from exposure logging, photographic documentation was made in the years of 2002–2004.

3. Locating of exposures (except for sites unknown to authors) in respect to the distinct lower boundary of the Menilite Formation and, when possible, versus well-defined chronohorizons, was performed in the course of detailed geological mapping. As a result, it was possible to prepare cross-sections through outcrops of the Menilite Formation and to reconstruct lithological sections, commonly drawn at scales of 1:1,000 or 1:2,000, rarely 1:500 or 1:3,000.

Standard methods of geological correlation aided by lithostratigraphic subdivision of the formations and marker horizons were used in construction of synthetic and composite sections. Detailed 1:5,000 and 1:10,000 maps of Błażowa-Borek Nowy, Krępak-Brzuska, and Leszczawa-Huta Poreba regions, prepared by the senior author for other purposes, were also helpful (Kotlarczyk, 1966, 1999; archival materials) along with papers dealing with lithostratigraphy and sedimentary environment of the Menilite Formation (Kotlarczyk, 1988; Kotlarczyk & Leśniak, 1990).

Detailed geological mapping of tectonically-complicated Przysietnica and Hłudno regions was performed specially for the purpose of this work to reconstruct genuine bed sequence of the Menilite Formation. During reconstruction of four sections, some data published by other authors (Kozarski & Szymakowska, 1961; Jucha, 1969; Gucik, 1988) were used. These will be referred to in subsequent chapters.

Descriptions of sections of the Menilite Formation paid particular attention to possible tectonic duplications or reductions (that was, e.g. the case of the Przysietnica section), as well as to bed distortion resulting from submarine mass movements. The latter observation helped to identify olistoliths of older members within younger strata like, for instance, at Hermanowa.

When reconstructing sections of the Krosno Formation, necessary to constrain stratigraphic position of infrequent ichthyofaunal sites of this formation and to understand lateral interfingering of the two discussed formations, both published (Kotlarczyk, 1966; Jucha, 1969; Rajchel, 1989) and archival data of the senior author were used.

Specialized methods used in realisation of the remaining tasks will be discussed in respective chapters when necessary.

MATERIAL

The presented collection of fossil fish comes from exposures of variable size, 1 m to several tens of metres large, and type. In most cases, these exposures are situated in river beds and their undermined slopes or road cuts, rarely in pits (poorly cemented sandstones), brickyards (claystones), quarries (sandstones, hard marls, cherts), and landslide scars. Exceptionally, solitary specimens have been derived

from logs of Łodygowice (IG-1) and Borek Nowy (IX-11) boreholes.

More numerous ichthyofauna-bearing exposures of the same locality were consecutively numbered or labelled by letters. Each exposure was given a code name, including place name-derived acronym and serial number, e.g. D, BR₆, B_m, PS_{5a}, BN_{IX-11} (borehole). Different ecological assemblages occurring within one exposure were discriminated by code names of lithological complexes, like: KT_{BD} and KT_{EF}, or abbreviations: WE_{bp} (bottom part) and WE_{up} (upper part).

All the localities and exposures are listed in Table 1 in an alphabetical order based on place name acronyms. Such ordering should help in identification of ichthyofaunistic sites, marked by their acronyms on the geological map (Fig. 1). The table includes the total number of specimens collected at every exposure of a given locality, taking into account specimens found on dump heaps. As already mentioned, not every sampled exposure was found, and some of them turned out to be destroyed. It means that not every ichthyofaunistically-exploited exposure possesses lithological description. Therefore, Table 1 lists the total length of sampled sections of exposures, separated into fully documented and undocumented ones.

Altogether, 1,366 m of sections were sampled, mostly of the Menilite Formation (the Krosno Fm. is represented by 20 m only), from which ca. 1,170 m bear lithological documentation. The real length of the sampled section was in fact greater, but numerous destroyed or unfound exposures lack proper data. The total number of exploited specimens is 13,011. Some of them (namely 259 specimens of Teleostei), however, have not been due to a number of reasons included into taxonomical composition of the collection which numbers 12,752 specimens. The number of specimens per exposure changes from 1 to 1,435.

This scatter results mainly from the time allocated to fish exploitation in an exposure, and less from the genuine frequency of occurrence. All exposures can be subdivided into three groups. The first group includes those exposures where exploitation was restricted to prospection purposes, i.e. identification of “fish-bearing” strata and estimating topographic and geological perspectives for further exploitation of more numerous assemblages. At such exposures, few specimens were collected only. The second group embraces exposures, at which exploitation for ecostratigraphic purposes was conducted. The collected assemblages usually numbered ten to twenty or a few tens of specimens. The third group, in turn, is represented by exposures rich in fish, exploited mainly for palaeontological material, and where the obtained assemblages were composed of hundreds of specimens.

The statistical distribution of the collected material is as follows (number of specimens per one exposure versus the number of relevant exposures): 1 to 2 specimens – 47 exposures, 3 to 10 vs. 71, 11 to 30 vs. 40, 31 to 70 vs. 28, 71 to 250 vs. 25, and more than 250 vs. 11. Forty-two exposures supplied more than 50 specimens each, and twenty-eight exposures numbered more than 100 specimens. The following exposures provided especially numerous specimens (the number of specimens per 1 m of sediment section is given in

Table 1

List of ichthyofauna-bearing localities and exposures (for location on geological map – see Fig. 1)

Acronym	Locality	Exposures	Number of specimens	Length of sampled sections (m)		
				Geologically documented	Geologically undocumented	Total
B	Błażowa	B ₁ , B ₂ , B ₃ , B ₄ , B ₅ , B ₆ , B ₁₅ , B _a , B _c , B _k , B _m , B _s	982*	47.7	10	57.7
BB	Bóbrka	BB ₁₀₄ , BB ₁₁₈	10	9.5		
BE	Brzezówka/ Hyżne	BE ₁ , BE ₂	18	12.8	2	14.8
BG	Błażowa - Ostra Góra	BG	1	~1.0		
BH	Bachów	BH ₁ , BH ₂ , BH ₃	1,903*	22.9	3	25.9
BK	Bandrów-Królowka	BK ₁ , BK ₂	6	?	?	
BN	Borek Nowy	BN ₃ , BN ₄ , BN ₅ , BN ₇ , BN _{7a} , BN _{IX-11}	58	9.0	3.5	12.5
BO	Brzozówka/Jedlicze	BO	9		~5.0	
BP	Babice-Połanki	BP ₁ , BP ₂	211	8.15		
BR	Brzuska	BR ₁ , BR ₂ , BR ₄ , BR ₅ , BR ₆ , BR ₁₀ , BR ₁₁ , BR ₁₉ , BR ₂₁ , BR ₂₂ , BR _{22a} , BR ₃₄ , BR ₃₉ , BR ₄₃ , BR ₄₅	278*	27.9	29	56.9
BW	Błażowa - Walant	BW	36		~3.0	
BZ	Bachów- Zadworze	BZ	8		~4.0	
C	Czerwonki	C	6	8.5		
CH	Chocnia	CH	30	12.5		
D	Dobra	D, D _a	84	30.6		
DG	Dobra Góra	DG	169	21.6		
DU	Dubnik	DU ₁ , DU ₂ , DU ₃ , DU ₄	31		6	
F	Futoma	F	23		3	
G	Górki	G	1		?	
H	Hłudno	H ₁ , H ₂ , H ₃ , H ₄ , H ₅ , H ₆ , H ₇ , H ₁₁₉ , H ₁₃₂	111	109.48		
HB	Huta Brzuska	HB ₁ , HB ₂ , HB ₃ , HB ₅ , HB ₆ , HB ₈	109*	22.8	6.5	29.3
HD	Hłudno	HD ₁ , HD ₂ , HD ₃ , HD _s	260*	27.85	1.5	29.35
HDK	Hłudno	HDK	15	20.5		
HE	Hermanowa	HE	16		~5.0	
HK	Hermanowa - Kamieniec	HK ₁ , HK ₂	55		~1.0	
HP	Huta Poręby	HP _a , HP _b	26*	13.1		
HT	Harta	HT	171	3.2		
J	Jamna Dolna	J _{AC} , J _{DG} , J ₁ , J ₂ , J ₃ , J ₄	925*	14.4		
JZ	Jazowa/Frysztak	JZ _a , JZ _b	10	?		
K	Krępak	KI, KI ₁ , KI _{1a} , KI ₂ , KI ₃ , KII, KII ₁ , KII ₂ , KII ₃ , KII _b , KII _c , KII _e , KII _h , KIII, KIV ₁₋₃ , KIV _{2a} , KIV ₄₋₅ , KI-g, K	1,314*	153.2	4	157.2
KC	Krościenko/Strwiąż	KC ₁ , KC ₂	3		~5	
KD	Krzemyk - Dynów	KD	13	2.4		
KK	Kąkolówka	KK ₁ , KK ₂	61	51.3		
KL	Klarowiec	KL	16	30.5		

Table 1 (continued)

Acronym	Locality	Exposures	Number of specimens	Length of sampled sections (m)		
				Geologically documented	Geologically undocumented	Total
KN	Kniażyce	KN ₁ , KN ₄	59	5.44		
KR	Krosno	KR, KR ₀	9	13.0		
KS	Końskie	KS ₁ , KS ₃	16		~3.5	
KT	Kotów	KT _{BD} , KT _{EF}	23	12.0		
KW	Krakowica - Inwałd	KW	1		~1.0	
L	Leszczawa	L, L ₁ , L ₄ , L ₇ , L ₁₀ , L _S	203	16.6		
LA	Laskówka	LA	27		~10.0	
Ł	Łodzinka Dolna	Ł ₁ , Ł _{1a} , Ł ₂ , Ł ₃	17	4.0		
ŁH	Łubno/Hłudno	ŁH ₁ , ŁH ₂	27		~3.0	
ŁŁ	Łubno-Łazek	ŁŁ ₁ , ŁŁ ₂	143		~4.0	
ŁW	Łodygowice	ŁW	3		?	
M	Malawa	M ₁ , M _{1a} , M _{2bp} , M _{2up}	45	19.1	0.5	19.6
MR	Mrzygłód	MR ₁ , MR ₂ , MR ₃ , MR ₄	8		7.0	
N	Nozdrzec	N	2		~1.0	
ND	Nowosiółki Dydyńskie	ND	4		~3.0	
NS	Nowe Sady	NS	20		~3.0	
O	Obarzym	O ₁ , O ₂ , O ₃	123	18.2	3.0	21.2
P	Przymiarki	P ₁ , P _{2bp} , P _{2up} , P ₃ , P ₄ , P ₆	257	30.6		
PB	Przedmieście Babickie	PB	27	11.5		
PŁ	Przysietnica-Łazek	PŁ	9		~3.0	
PP	Piątkowa Polska-Łęg	PP	1		?	
PR	Pererowce - Dobra	PR	2		1.0	
PS	Przysietnica	PS ₀ , PS ₁ , PS ₂ , PS ₃ , PS _{3a} , PS ₄ , PS ₅ , PS _{5a} , PS ₆ , PS _{6a} , PS ₇ , PS _{7a} , PS ₈ , PS _{8a} , PS _{8b} , PS ₉ , PS ₁₀ , PS _{II}	2,548*	35.3	14.5	49.8
PT	Piątkowa	PT ₁₋₃	35*	2.45		
PW	Pawłokoma	PW	1		0.5	
R	Równe	R ₁ , R _{4bp} , R _{4up}	133*	23.75		
RB	Rudawka (Birczańska)	RB, RB _{1bp} , RB _{1up} , RB ₂ , RB ₃ , RB ₄	87	31.8	5	36.8
RO	Rogi	RO ₁ , RO ₂	537*	22.6	2.0	24.6
RR	Rudawka Rymanowska	RR ₁₋₃ , RR ₄ , RR _{4a} , RR _{4b} , RR ₀₃	122*	79.5		
RT	Ratny Potok - Dobra	RT	4		2.0	
S	Straszędzie	S ₁ , S _{1a} , S _{1b} , S ₂ , S ₃ , S ₄	232	53.3	3.0	56.3
SE	Siemowica	SE ₁₂ , SE ₁₃ , SE _{II}	53	9.7	6.0	15.7
SK	Skopów	SK	251*	5.95		
SO	Sobniów	SO	351		~3.0	
SR	Średnia	SR	12	5.0		
ST	Stebnik	ST	10		~5.0	
T	Temeszów	T ₁ , T ₂ , T ₃ , T ₄	64	29.4	5.0	34.4

Table 1 (continued)

Acronym	Locality	Exposures	Number of specimens	Length of sampled sections (m)		
				Geologically documented	Geologically undocumented	Total
U	Ulanica	U	2		~2.0	
W	Winnica	W	139	8		
WE	Wola Węgierska	WE _{bp} , WE _{up} , WE _O	333*	32.3	2.0	34.3
WJ	Wojtkowa	WJ _{1-1a} , WJ ₂	12		~4.0	
WW	Wisłok Wielki	WW ₁ , WW ₂	35	39.0		
WZ	Wujskie/Załuż	WZ, WZ ₃ , WZ ₆ , WZ ₉ , WZ _{up}	44		8.0	
Z	Załuż	Z	3		?	
ZH	Zahuty/Huta Poręby	ZH	9		~1.0	
		Total	13,011	1168.37	197.5	1365.87

bp – bottom part of exposure, up – upper part of exposure, * – including specimens collected from dump heaps at some exposures

brackets): Przysietnica – PS_{5, 5a}: 1,435 (174); Bachów – BH₁: 1,291 (538); Jamna Dolna – J_{AC} + J_{DG}: 909 (68.3) [J_{AC}: 303 (47) and J_{DG}: 571 (83)]; Krępak – KII₃: 575 (42); Błażowa – B₄: 545 (22); Rogi – RO₁: 497 (22); Bachów – BH₃: 488 (24); Przysietnica – PS₇: 397 (256) and PS_{8a}: 326 (163); as well as Sobniów – SO: 351 (117).

High specimen frequency per 1 m of sediment section was also obtained at some of those localities which provided smaller number of specimens, like, for instance: Skopów – SK: 251 (42); Babice – Połanki – BP₂: 207 (46); Harta (Krosno Formation) – HT: 171 (53); Błażowa – B_a: 169 (43); Przymiarki – P₄: 159 (40); Łubno-Łazek – ŁŁ₁: 139 (139); Hermanowa – Kamieniec – HK: 55 (55); Przysietnica – PS₃: 45 (45), as well as Brzuska – BR₄: 67 (32) and BR₅: 65 (27); PS₂: 30 (30); Leszczawa – L: 73 (24); and Błażowa – B₁: 126 (21).

Numerous specimens were supplied owing to prolonged exploitation of the Jasło Limestones at ŁŁ₁, SO, PS₃, and PS₂, basal cherts of the Menilite Formation at SK, J_{AC}, and WE_{bp}: 185 (66), as well as the upper part of this formation, including younger portion of the upper bathypelagic assemblages, at exposures: BH₁, B_a, KII₃, BR₄, BR₅, BH₃, BP₂, and B₄. Exploitation of sediments bearing the neritic-sublittoral assemblage, in turn, seldom provided high specimen frequency, like, e.g. at Jamna Dolna – J_{DG}, Rogi – RO₁, Przymiarki – P₄ and Leszczawa – L: 73 (24). Usually, the specimen frequency did not exceed ten to twenty specimens per 1 m, even at exposures bearing more numerous assemblages, like: Winnica – W: 139 (17), Wola Węgierska – WE_{up}: 140 (5), Równe – R₁: 91 (7), Dobra Góra – DG: 169 (8), Dobra – D: 79 (3), and Rudawka Rymanowska – RR₁: 104 (2). One can infer, therefore, that fish of the neritic-sublittoral assemblage were less numerous in the basin, because the state of skeleton preservation was more or less the same. It should also be mentioned that the highest number of specimens per 1 m of sediment, both in the neritic-sublittoral (J_{DG}) and bathypelagic (PS_{5, 5a}) assemblages, results from the presence at the two exposures of

a thin layer rich in ichthyofauna, pointing to the occurrence of isolated ecological events. Excluding these layers from further calculations, the number of specimens per 1 m of sediment decreases to 42 and 98 at exposures J_{DG} and PS_{5, 5a}, respectively. Of particular importance is high frequency of specimens representing the upper bathypelagic assemblage in the Subsilesian Unit, like at Przysietnica: PS_{5, 5a}, PS₇, PS₈.

In most cases, the number of specimens per 1 m of sediment does not exceed 10. High frequency observed at the above-mentioned 20–30 exposures influences the average number of specimens per 1 m, calculated for all the sampled sections at more than 9.

The Dukla Unit is represented by 1 exposure only (WW, with 35 specimens); the Silesian Unit – by 20 exposures at localities: BB, BO, G, KL, KR, ŁW, R, RO, RR, SO and W, with 1,330 specimens; the Subsilesian Unit – by 21 (23) exposures at localities: JZ, PS, WZ, Z, and – probably – CH and KW, with 2,645 specimens; whereas the Borysław-Pokuttya Unit includes 8 exposures at localities: DU, KN, NS, ND, supplying 114 specimens. The remaining 171 exposures, supplying in total 8,887 specimens, are situated in the Skole Unit.

OUTLINE OF STRATIGRAPHY OF THE MENILITE-KROSNO SERIES

Lateral interfingering of a facies of brown-black, usually noncalcareous shales of the Menilite Formation (MF_m) with that of ash-grey, strongly calcareous and micaceous sandstones and shales of the Krosno Formation (KF_m), documented nearly half a century ago (Jucha & Kotlarczyk, 1958, 1959, 1961; Shakin, 1958; Koszarski & Żytko, 1959, 1961), is of fundamental importance for the stratigraphy of the Menilite-Krosno Series (MKS). Further stratigraphic details were described at large by Jucha (1969), Kotlarczyk (1966, 1980), and Korab and Kotlarczyk (1977), whereas

EPOCH	AGE	NANNO-FOSSIL BIOZONES (Martini, 1971)	TECTONIC & FACIES UNITS																	
			DUKLA	SILESIA	SUB-SILESIA	SE AREA (INNER PART)	SE AREA (OUTER PART)	NW AREA	BORYSLAV-POKUTTYA											
EARLY MIOCENE	BURDIGALIAN	1					POLYANYTSYA MEMBER	LESZCZAWKA MBR	JAWORNIK RUSKI MEMBER											
							2	DYDNIA MEMBER												
		NN4	NN3	NN2	?				CAPOR MEMBER											
		NN2							NIEBYLEC MEMBER											
		NN1	NP25			KROSNO FORMATION			JUTNA MEMBER	KORZENIOWKA MEMBER	BLAZOWA MEMBER	OLIWNA GORA MEMBER								
		NP24				KROSNO FORMATION			LOPYANKA MEMBER	HUTA BRZUSKA MEMBER		KORZENIOWKA MEMBER								
OLIGOCENE	RUPELIAN	NP23						KREPAK MEMBER	KLIWA MEMBER	PRZYLASEK OLIST.										
											UPPER MENILITE BEDS	BOREK NOWY MEMBER	KREPAK MEMBER	MAKLUCZKA MEMBER	KREPAK MEMBER	NOWOSIOLKI DYDYSKIE MEMBER				
																	KROSNO FORMATION	RUDAWKA TRACTIONITE MEMBER	FUTOMA MEMBER	HUVNIKI MBR
											CERGOWA MEMBER	DYNOW MEMBER	CHERT MEMBER	BORYSLAV MEMBER	SIEDLISKA MEMBER	JAMNA DOLNA MEMBER				
SUBCHERT MEMBER	MSZANKA MEMBER	PAPIN MEMBER	GLOBIGERINA	MARL = STRWIAZ	MARL MEMBER	BORYSLAV MEMBER	SIEDLISKA MEMBER	JAMNA DOLNA MEMBER	BORYSLAV MEMBER	POPIELE OLIST.										

Fig. 2. Lithostratigraphy of the Menilite-Krosno Series (MKS) in the eastern part of the Polish Carpathians (compiled by J. Kotlarczyk, this paper). Correlation with calcareous nannoplankton zones based on biostratigraphic studies of different authors, discussed in the text. The third column shows two options regarding the age of younger members of MKS, including (I) and excluding (2) some of the debatable radiometric dates. Marker horizons: G – Gąsiorów Tuff Horizon; T – Tylawa Limestone Horizon; W – Wujskie Limestone Horizon; J – Jasło Limestone Horizon; U – Upper Chert Horizon; K – Końskie Tuff Horizon (t.IV); D – Dobrzanka Tuff Horizon (t.V); B – Bądrów Tuff Horizon (t.VI); Ki – Kiczera tuff; sample 36 (t.VII); K₃₇ – Krzywe tuff, sample 37 (t.VII). Brown colours denote Menilite facies (light brown shade marks sandstone members), shades of yellow indicate Krosno facies (darker shade marks shale member)

synthetic overviews were presented by Kotlarczyk (1985, 1988a, 1988b) and Koszarski (1985).

Stratigraphic terminology of both these formations includes numerous informal names. Some of them have proved useful and require formalisation, while others do not meet lithostratigraphic requirements and should be abandoned.

Some of old, informal lithostratigraphic names like, for instance, the lower, middle and upper Krosno beds have been used in a different sense, i.e. indicating temporal subdivision of the formation irrespectively of its lithostratigraphy (Koszarski & Żyto, 1961). Moreover, it was practically impossible to mark the boundaries of such defined subdivisions over a large area occupied by the formation.

A collection of Oligocene–Early Miocene fish has been assembled from the two described formations within several tectonic units of the Outer Carpathians, i.e. the Dukla (DU), Silesian (SU), Subsilesian (SSU), Skole (SKU), and Boryslav-Pokuttya (BPU) units (Fig. 1).

Lithostratigraphy

A lithostratigraphic scheme of the Menilite-Krosno Series within the above tectonic and facies units will be presented below. The scheme was established owing to many years of studies (Kotlarczyk, 1966, 1988a, 1988b; Kotlarczyk & Leśniak, 1990) and became supplemented for the purpose of this work. This scheme (Fig. 2) shows spatial-temporal relationships between the two formations and distinguished members, irrespectively of their thicknesses. These relationships are referred to the discovered chronohorizons, represented by the laminated Jasło Limestones, tuff horizons, and other features (Kotlarczyk, 1980).

The MKS is commonly considered to begin with the so-called sub-chert beds which are underlain by a horizon of the Globigerina Marls (cf. Leszczyński, 1997), ubiquitous throughout the Carpathians. However, in the innermost part of the basin (DU), the Globigerina Marls are replaced by a sequence of calcareous and micaceous sandstones and shales of the Krosno facies including intercalations of the Menilite-type shales, distinguished as the so-called Papin beds (cf.

Korab & Kotlarczyk, 1977). These represent the oldest element of MKS. Deposition of the Menilite-Krosno facies sediments was the shortest in DU and the longest in the outer part of the basin (the lack of the youngest portion of MKS within BPU in Poland results from tectonic reduction). The most detailed lithostratigraphic scheme is characteristic of the Skole Unit, where different development of MKS in different parts of this unit was taken into account.

The oldest horizon of the Menilite Fm. from which fish were exploited are the sub-chert beds. These are clayey, alternately green and brown, frequently marly shales, rich sometimes in *Planorbella* detritus. In the Skole Unit, these beds are called the Jamna Dolna Member. In an area limited to channel zones of submarine fans there occur sequences of sandstones and conglomerates, intercalated by brown, clayey and marly Menilite shales, distinguished as the Siedliska Member, or thick-bedded, noncalcareous, whitish quartz arenites representing grainflows, distinguished as the Boryslav Member. The lower part of the sub-chert beds are replaced by the sandstone-dominated Mszanka Member in DU, and by the Popiele Member of olistostrome character in BPU (Dżułyński & Kotlarczyk, 1965).

These lithologically differentiated members are overlain by a thin, although extensive sequence of diagenetic cherts (originally diatomites), called the Kotów Member. Higher up there occurs a vast and thin packet of bedded turbiditic marls, called the Dynów Member, which in DU is known as the sub-Cergowa Marls or Jawornik Member (Ślącza, 1970).

In DU and the southern part of SU, the upper part of the Dynów Marls and the lowermost portion of the overlying Menilite shales become replaced by a sandstone-shaly sequence of the Krosno facies, distinguished as the Cergowa Member. The overlying shales, mudstones and less frequent thin-bedded sandstones are informally called the upper Menilite beds/shales. These are replaced in the southern part of DU by the Krosno Formation. In the remaining part of SU, the Menilite Formation overlying the marly horizon has not been subdivided into members.

This part of the Menilite Fm. is replaced in more outer units by the widespread Rudawka Tractionite and Borek Nowy Sheet-like Shale members, along with locally occurring: Huwniki Quartzarenite, Futoma Diatomite, and Nowosiółki Dydyńskie Mudstone members. Shortly above the Dynów Mbr and within deposition area of the Cergowa Mbr, in transitional beds of the latter member and the upper Menilite beds, a mega-horizon (numbering between ten and twenty layers) of the laminated Tylawa Limestone occurs.

In SSU, a sequence of alternately brown and greenish-grey, clayey-cherty, banded shales occurs above the Borek Nowy Mbr. An analogous sequence was described from the Subsilesian-Ždanice Unit of the Moravian Carpathians as the Šitbořice Member (Stranik, 1981). This name has been used in this paper in a sense applied by Krhovský (1991), i.e. excluding the lower, 4-m-thick sequence of slumped beds which are probably equivalent to the Rudawka and Borek Nowy members.

The lower part of the Šitbořice Member includes several layers of laminated limestones of the Jasło Limestone type, although occurring ca. 40 m below the Jasło Lime-

stone Horizon. It is proposed to call these limestones the Wujskie Limestone Horizon.

In SKU, the Borek Nowy Mbr is overlain by strongly differentiated sediments. This facies differentiation results from the presence of different sedimentary environments (e.g., basin slope and bottom, channel and interchannel zones, distal parts of a few submarine fans) and different source areas. Such conditions prevent distinguishing members of a broader extent and result in incomplete subdivision of the Menilite Formation. Correlation of individual members within so differentiated lithostratigraphic subdivision is only possible due to the presence of the Jasło Limestone and upper chert horizons, and a sequence of light-green shales.

The Jasło Limestone megahorizon is understood in this paper as an assemblage of all limestone layers separated by other lithotypes, irrespectively of the fact that sometimes three clusters of limestones can be distinguished. All limestone layers were deposited in a very short time and their palaeontological discrimination is not possible. Therefore, distinguishing the upper cluster as the Zagórze Limestone (Haczewski, 1989) appears redundant, as far as stratigraphic purposes are concerned.

The upper chert horizon, less clearly marked in Poland, can easily be traced in the Eastern Carpathians (cf. Jucha, 1969).

A sequence of green shales distinguished as the Krępak Member (Kotlarczyk, 1988a) appears in different parts of the study area, also in the form of thin layers which separate beds of white quartzarenites (grain flows) that are lithologically similar to the Kliwa Sandstones, known from the Eastern Carpathians (Kotlarczyk & Leśniak, 1990). The Kliwa Sandstones occur below the Jasło Limestone in their stratotype area on the Prut River. To maintain this name, although in its lithostratigraphic sense, it was decided to separate the Kliwa Member from the Krępak Member (*sensu* Kotlarczyk & Leśniak, 1990), as a local substitute of the latter (Fig. 2).

In the NW part of the area, the Krępak and Kliwa members are replaced by the Makłuczka Member (Kotlarczyk & Leśniak, 1990), composed of brown shales bearing intercalations of green shales.

The Kliwa Member is overlain by the Huta Brzuska Member (black shales, cohesive mud-sandy flows of the Jawornik Ruski Sandstone-type), introduced first in this paper, the Lopyanka Member (calcareous flysch of the Krosno facies, intercalations of brown shales), and the Korzeniówka Member (brown, noncalcareous and calcareous shales, thin-bedded quartz arenites, rare intercalations of Kliwa-Krosno and Krosno sandstones, subordinate cherts), also first introduced in this paper.

In a more inner part of the SE area, the upper part of the Huta Brzuska Member is replaced by the lower part of the Lopyanka Member, whereas the upper part of the Korzeniówka Member is replaced by the Jutna Member, which is composed of thick-bedded sandstones and shales of the Krosno facies with rare intercalations of frequently marly Menilite shales.

In the NW area, the Krosno facies is absent from the Menilite Fm. until the very top of the latter; hence, the

above-mentioned lithostratigraphic members cannot be distinguished. An unnamed portion of the Menilite Fm. overlying the Przylasek Mbr olistostrome is composed of brown shales intercalated by the Kliwa-type sandstones. Higher up, the upper chert horizon is to be found. In a fragment of this area, the increasing amount of sandstones has been distinguished as the Błazowa Member.

In BPU, the Menilite Fm. overlying the Nowosiółki Dydyńskie Mbr is strongly lithologically differentiated, preventing further detailed subdivision into members. A characteristic feature is a large amount of green, greenish-grey and grey shales which intercalate brown shales. Individual segments of the Menilite Fm. section resemble, in this respect, those of SSU. The lower intercalation of green shales is equivalent to the Krępak Mbr; the topmost one has been distinguished as the Oliwna Góra Member. In the medial segment of the section, both below and above the Jasło Limestone Horizon, frequent intercalations of grey, calcareous and micaceous shales are accompanied by the Krosno-type sandstones. These strata have been named the Lopyanka Member. The Krosno facies sediments appear here earlier than in SKU. The upper segment of the Menilite Fm. reveals properties of the Korzeniówka Mbr, including, i.a. the upper chert horizon which is accompanied by thin layers of the laminated Jasło-type limestone.

Another characteristic feature of the Menilite Fm. within BPU is ubiquitous occurrence – at different stratigraphic levels – of submarine slumps, cohesive mudflows bearing exotic rocks, and conglomerates which are indicative of deposition on the upper basin slope. Tectonic contacts between exposures of the Menilite Fm. prevent reconstruction of the section of younger sediments which, in turn, occur farther southeastwards in this unit.

In the studied portion of the Skole Unit, the base of the Krosno Fm. is marked by the Niebylec Shale Member. These strata include the ubiquitously occurring Końskie Tuff Horizon (Sikora *et al.*, 1959), and the not so extensive Piątkowa Diatomite Horizon (Kotlarczyk & Kaczmarek, 1987). The higher part of the Krosno Fm. is composed of normal flysch strata, including intercalations of thick-bedded sandstones. This sequence, previously called the middle Krosno beds, are proposed to be distinguished as the Capor Member. In the central part of the study area, this member is overlain by a shaly sequence (previously known as the upper Krosno beds) which are now distinguished as the Dydnia Member. Both these members are linked by a 1–3-m-thick tuff layer (V horizon of Sikora *et al.*, 1959), also described as the Main Tuff Horizon by Kotlarczyk (1966). It is proposed to call this horizon in the present paper as the Dobrzanka Tuff Horizon. In the inner portion of the SE area, the higher-situated (VI) Bandrów Tuff Horizon was found in one of the sections (Sikora *et al.*, 1959).

The Leszczawka Diatomite Member, mostly of olistostrome type (Kotlarczyk, 1983), overlies either Dydnia or Capor members. Among numerous (up to 8) tuff intercalations in this member, the basal Kiczera Tuff Horizon (3.8 m thick) and the topmost Krzywe Tuff Horizon (2–3 m thick), together representing the VII tuff horizon of Sikora *et al.* (1959), should be mentioned. In the Leszczawka Syncline (Fig. 1), the lower part of this member is replaced by a se-

quence of noncalcareous sandstones deposited by cohesive sandy-mud flows, and called the Jawornik Ruski Member.

The Krosno Fm. section in SKU terminates with a 20–40-m-thick sequence of shales, called the Polyanytsya Member (Kotlarczyk, 1988a).

The contact between the Menilite and Krosno formations in the studied portion of SSU is of tectonic character. Neither the Niebylec Mbr, nor equivalents of shaly members nor diatomites have been found.

In the marginal, northern part of SU the most probable equivalent of the Niebylec Mbr appears to be one of the topmost shale sequences of the Krosno Fm. (Koszarski, 1985; Koszarski *et al.*, 1995); although bearing no traces of the IV tuff horizon. It is likely that this position is occupied by a tuff layer found at Radziszów south of Kraków (Fig. 1), in the Krosno Fm. strata that build the marginal part of SU (Książkiewicz & Wieser, 1954).

Bio- and chronostratigraphy of the Menilite-Krosno Series

Biostratigraphical studies of the Menilite-Krosno Series have raised serious difficulties, mostly due to: (1) limited occurrence of calcareous plankton and nannoplankton; (2) rare appearance of index taxa of the former, necessitating determination of substitute taxa; (3) frequently observed first appearances of stratigraphically important taxa in undoubtedly different positions, in nearby sections; (4) very intensive redeposition of fossils, preventing the use of LADs and limiting reliability of FADs of individual taxa.

Such situation has led to selective, detailed elaboration of some of lithostratigraphic members and limestone horizons. Up to now, most of these members have only been given preliminary zonal characteristics.

One of well described horizons is that of the Globigerina Marl (Strwiąż Mbr *sensu* Rajchel, 1990), assigned to NP19–20, NP21 and the lower part of NP22 zones (Oszczypko-Clowes, 1998; cf. also references in: Leszczyński, 1997), which are equivalent to P15_(upper part), P16, P17 and P18_{lower part} foraminiferal zones (according to Berggren *et al.*, 1995). Therefore, the base of the Oligocene, situated between P17 and P18 zones, is placed within the Strwiąż Mbr. The age of this boundary, previously determined at 33.7 Ma (Berggren *et al.*, 1995), has recently been corrected to 33.9 (±0.1) Ma (Gradstein *et al.*, 2004). An Oligocene age has also been indicated for the Siedliska Mbr (Blaicher & Nowak, 1963a).

Another calcareous member, the Dynów Marl Mbr, is mainly composed of coccolith turbidites and contains assemblages of NP23 zone (Krhovský, 1981), as has been later confirmed in the Moravian Carpathians (Krhovský, 1998). A slightly older age, referring to the upper part of NP22 zone, was determined by Dudziak (in: Smoleńska & Dudziak, 1989) for the Jawornik Mbr in DU. The determination appears probable, because this member is equivalent to the lower part of the Dynów Mbr, although not a decisive one since it is based on LAD of *Reticulofenestra umbilica*.

Determination of the age of the Jasło Limestone Horizon for NP24 zone (Krhovský, 1981; Gaździcka, in: Kot-

larczyk, 1988a; Jugowiec, 1996) is a very important finding. This determination is based on the presence of a substitute taxon *Cyclicargolithus abisectus*, the FAD of which was assigned to the beginning of NP24 zone. The dating has been confirmed by the results of studies of the Jasło Limestones in the Moravian Carpathians (Bubik, 1987), although later determinations appear to indicate the top of NP23 zone (Bubik, 1992).

The presence of NP23 and lower part of NP24 zones, as well as the corresponding foraminiferal biozones P20 and P21, has been documented in the Šitbořice Mbr, in SSU of the Moravian Carpathians (Bubik, 1987; Krhovský, 1998).

Two assemblages have been found above the Jasło Limestone Horizon in the Lopyanka Member of the Eastern Carpathians. The lower assemblage with *Globigerina ampliapertura*, and the upper one with *G. ciperoensis* and *Paragloborotalia opima opima* have been assigned to zones NP24 and NP25, respectively (Gruzman, 1984). In SU south of Lesko (Fig. 1), within the Krosno Fm. situated above the Jasło Limestone, Garecka *et al.* (1999) found nannoplankton assemblages which could indicate the presence of NP24 (and NP25?) zones, whereas the uppermost sequences of this formation in the same area turned out to bear taxa indicative of NN1 (*Helicosphaera scissura*) and, perhaps, NN2 (*H. ampliapertura*) zones, provided that their FADs in this area were not older.

Dating of the Niebylec Mbr is a very important issue. Nowak *et al.* (1985) and Gasiński *et al.* (1986) found out that the age of this member should be referred to foraminiferal subzones N4b and N4c with *Globigerinoides immaturus* and *Globoquadrina dehiscens*, which are coeval with the lower part of NN2 biozone (*sensu* Berggren *et al.*, 1995). The Piątkowa Diatomite Horizon includes, apart from Oligocene taxa, also Early Miocene diatoms (Kotlarczyk & Kaczmarek, 1987). Thus, the Oligocene/Miocene boundary occurs at the base of the Niebylec Mbr or, more probably, lower.

Subsequent works on calcareous nannoplankton of this member led Ślęzak *et al.* (1995a) to conclude about its younger age. The stratotype section of the member was placed within NN2_{upper part} and NN3_{lower part} biozones, although at Końskie section the Niebylec Mbr was dated to NN2 zone only (Ślęzak *et al.*, 1995b). Detailed discussion on this discrepancy and unconvincing reasoning in favour of the presence of NN3 zone goes beyond the scope of this paper.

It should be taken into account, however, that specimens of *Sphenolithus belemnos*, reported from the Niebylec Mbr stratotype section and allegedly indicating the presence of NN3 zone (or the topmost part of zone NN2), could in fact represent a form transitional between *S. dissimilis* and *S. belemnos*, described as *S. disbelemnos* (Fornaciari & Rio, 1996) after the authors' paper was published. FAD of this taxon marks the beginning of NN2 zone (cf. Young, 1998). In addition, the presence of *Helicosphaera walbersdorffensis* in this assemblage does not prove the existence of zone NN3, since the authors themselves shifted FAD of this taxon from zone NN5 to NN3. Therefore, it can easily be lowered to zone NN2. All these facts appear to suggest that age estimations of the Niebylec Mbr based on calcareous plankton and nannoplankton can lead to comparable results.

Dating of higher-situated sequence of the Krosno Fm. ("middle Krosno beds") gave no unequivocal results. These were assigned to NN3 zone (Ślęzak *et al.*, 1995b), although it cannot be excluded that they also represent a part of – lasting more than 4 Ma – biozone NN2. Only the lower part of a shaly sequence of the "upper Krosno beds", i.e. the Dydnia Mbr, can most probably be linked with NN3 biozone, due to appearance in the upper part of this member of *Sphenolithus heteromorphus*, indicating the lower part of NN4 zone. A relationship between the lower part of this member and zone NN3 is additionally supported by radiometric age of the Bandrów Tuff (VI horizon) which occurs in that part of the sequence.

Samples collected close to the Leszczawka Mbr yielded *Globoquadrina dehiscens*, *G. langhiana*, *Turborotalia obesa* and other foraminifers which indicated a Burdigalian age (Gucik & Strzępka, 1986). A similar assemblage was also found within the Polyanytsya Fm. in the Eastern Carpathians, and in the uppermost part of the "upper Krosno beds" in the internal part of SKU, close to the gypsum horizon (Gruzman, 1984). Its age was determined to the Eggenburgian. The presence of dispersed gypsum detritus in the Polyanytsya Mbr (Kotlarczyk, 1962, 1980), most probably redeposited from littoral lagoons, links this member with the above-mentioned gypsum horizon and gypsum deposits of the lower Vorotyshcha Fm., dated to the Late Eggenburgian (Bobrinskaya *et al.*, 1998).

In the internal part of SKU in Poland, the uppermost sequence of the "upper Krosno beds", composed of the upper Dydnia Mbr, Leszczawka Mbr, and Polyanytsya Mbr, includes an assemblage of nannoflora with *Sphenolithus heteromorphus* and *Discoaster variabilis* (co-existing everywhere in zones NN4 and NN5), although devoid of *Helicosphaera ampliaptera* (Ślęzak *et al.*, 1995b). The absence of the latter taxon, whose LAD refers to the top of NN4 zone, led Ślęzak *et al.* (1995b) to conclude that the studied sediments already represented NN5 zone of Late Langhian age. This conclusion is in contrast to the authors' promise that they would use "the first appearance of stratigraphic markers as the only reliable criterion for zonal assignment" (*op. cit.*, p. 270). Proper interpretation, therefore, should lead to a conclusion that there is hardly any evidence for the presence of zone NN5 and that deposition of the discussed sediments terminated in zone NN4, most probably in the Late Otnangian or Early Karpatian. A supporting piece of evidence is the presence within the Pavlovice Formation (Moravian Carpathians), dated to the Otnangian (Krhovský, 1998), of a diatomite horizon which is correlatable with the Leszczawka Mbr.

An attempt at tephrostratigraphy

Stratigraphic applicability of numerous tuff horizons within the Menilite-Krosno Series have raised great expectations. The importance of some widespread and easily field-traceable tuff chronohorizons has already been mentioned above. Attempts were made to identify individual horizons basing on their mineralogical properties (heavy mineral composition, chemistry of plagioclases, morphometry of zircons, etc.), and to correlate tuff occurrences representing the same horizon (Wieser; in: Sikora *et al.*, 1959). At the

beginning, seven tuff horizons (I–VII) were distinguished and characterised; later studies, including also older formations, helped to distinguish 31 horizons, including 12 (numbered 19 through 31) within the Menilite-Krosno Series (Wieser, 1985).

This tephrostratigraphy was based on isotopic age determinations made by Ch. Naeser on zircons separated from tuffs of selected horizons. The results published by Van Couvering *et al.* (1981) and Wieser (1979, 1985) are listed in Table 2.

A normal stratigraphic succession is disturbed by the Kiczera and Krzywe 36 tuffs. That is why Koszarski (1985) and Wieser (1985) decided to eliminate these tuffs from the list of tuff horizons. On the other hand, the age of the youngest tuff (Krzywe 37) is estimated at the earliest Langhian what, taking into account the Carpathian tectogenesis and development of the foredeep, is hardly possible and calls for rejection of this date (Kotlarczyk, 1988a). Nowak *et al.* (1985) and Vass and Balogh (1986), in turn, accepted the discussed age estimation, although considering the lower age limit only. The age of the latter makes it possible to assign tuff deposition to the Karpatian. Following this way of reasoning, Kotlarczyk (1988a) considered acceptance of modified dates of the Kiczera and Krzywe 36 tuffs.

Taking into account the upper age limits, necessitating thereby shifting the age of the Bandrów Tuff towards the lower age limit of its interval, we obtain the following ages of successive tuff horizons: 19 Ma – Bandrów, 18.9 Ma – Kiczera, and 18.7 Ma Krzywe 36, all of them indicating the Otnangian.

Such a procedure is justified by an example of the Znamirowice-Gąsiory Tuff (lower layer) in the sub-chert beds of the Menilite Fm. in SU. Precise age estimation of the top and bottom of the Globigerina Marl, obtained due to dating of calcareous nannoplankton biozones (see above) at 32.7 Ma and 36.0 Ma, respectively, implies that the 34.6 Ma tuff should occur within the marls, and not in the centre of the overlying member (see also Leszczyński, 1997, table 3). It is only after the upper age limit is taken into account, when the tuff position resulting from its age approaches that it really occupies. Unfortunately, this approach is not sufficient enough in case of the higher-situated tuff layer (Znamirowice) in the same member. The lower age limit places this tuff at the boundary of zones NP23/24, i.e. close to the Jasło Limestone Horizon which – in SU – is situated fairly high, within the Krosno Fm. That is why the tuff was also eliminated from the list of tuff horizons (Wieser, 1985).

Another question requiring explanation is identification of the V tuff horizon in the studied SKU area with the Radziszów Tuff, which was found in a stratigraphically uncertain position within the Krosno Fm. of SU, near Kraków (Książkiewicz & Wieser, 1954). Even the age of the V tuff horizon, i.e. 20.5 Ma, raises a question of a wide time-gap (2.1 Ma) in respect to the age of the Bandrów Tuff, which is situated 100 m higher. If that is so, the rates of sedimentation of flysch sediments, quickly infilling the basin at that time, should have attained 0.05 mm/year only. Other doubts can be raised as well.

1. The chemical composition and structure of plagioclases of both tuff horizons are different. The Radziszów

Table 2

Radiometric ages of some tuff horizons in the Menilite-Krosno Series
(based on T. Wieser's papers cited in the text)

Name of horizon	Sample number	Number of horizon		Radiometric age Ma	Age brackets	Biozones marking boundaries of the age interval
		1959	1985			
Krzywe	37	VII	31	15.6 ± 1.1	16.7 - 14.5	NN4 - NN5
Krzywe	36	VII	-	19.8 ± 1.1	20.9 - 18.7	NN2 - NN3
Kiczera	-	VII	-	22.3 ± 3.4	25.7 - 18.9	NN25 - NN3
Bandrów	34/5	VI	30	18.4 ± 1.1	19.5 - 17.3	NN2 - NN4
(Dobrzanka)*	-	V		?		
Radziszów	33	V(?)	29	20.5 ± 0.9	21.4 - 19.6	NN2
Znamirówice	upper layer	-		28.9 ± 1.2	30.0 - 27.8	NP23/24 - NP24
Znamirówice-Gąsior	lower layer	-	19	34.6 ± 1.4	36.0 - 33.2	NP18/19 - NP21

* name introduced in this paper for horizon V

Tuff contains 53 to 54% of An which, in the inner part of crystals, increases up to 76% (Książkiewicz & Wieser, 1954). Analogous figures for the V horizon are between 30 and 40% (Sikora *et al.*, 1959).

2. T. Wieser considered oxyhornblende (lamprobolite) as an index mineral of the V tuff horizon, and basing on this finding assigned tuff occurrence at Kuźmina to this horizon. However, the Kuźmina locality bears only one tuff layer of the VII horizon (tuffs of this horizon at Kiczera also include hornblende among components of the “crystalline phase”; cf. Kotlarczyk, 1966). This mineral was found in tuffs belonging to two different horizons; hence, it is likely that it can also be found in another horizon, like the Radziszów Tuff.

In light of these remarks one should not correlate the Radziszów Tuff with that of the V horizon. The latter is proposed to be called the Dobrzanka Tuff in this paper (previous name “Main Tuff Horizon”, cf. Kotlarczyk, 1966, 1988a). This most extensive tuff horizon lacks radiometric dating. If age determination of the Bandrów Tuff horizon is correct, the age of the V horizon, which occurs ca. 100 m below (K. Żytko, *pers. comm.* 2005), can be estimated at ca. 18.6 Ma, given that the rate of flysch deposition was 0.5 mm/year.

Therefore, radiometric age determinations are of little value in the Carpathian conditions (redeposited tuffs were likely to have been contaminated by detrital zircons) and should not be relied upon, unless confronted with biostratigraphic data.

The age of the Radziszów Tuff is placed within the interval occupied by NN2 zone which, as shown above, occurs in SU within the youngest strata of the Krosno Fm. It is worth to note that the emended to the lower boundary of the uncertainty interval age of the Radziszów Tuff (21.4 Ma) is close to that of the IV tuff horizon, interpreted from the age of the Niebylec Mbr and – more precisely – 4Nc plankton zone, dated at ca. 21.6 Ma.

The most difficult task is to tune radiometric ages with biostratigraphic data pertaining to the uppermost part of the Krosno Fm. within SKU. Two options can be considered: including all radiometric ages, and eliminating some of them.

1. Corrected isotopic age determinations of the Kiczera (18.9 Ma) and Krzywe 36 (18.7 Ma) tuffs fall within the limits of NN3, zone, i.e. the turn of the Late Eggenburgian and Ottangian (Rögl, 1998). The emended age of the Bandrów Tuff (min. 19.0 Ma; max. 19.5 Ma), occurring ca. 400 m below the Krzywe 37 Tuff, is situated in the upper part of NN2 zone (Late Eggenburgian), like unknown, although older by ca. 0.2 Ma, age of the Dobrzanka Tuff. The corrected age of the youngest Krzywe 37 Tuff (16.7 Ma) refers to the mid-NN4 zone, i.e. the Karpatian (cf. Rögl *et al.*, 2003). The age of the youngest Carpathian strata inferred from these corrected determinations does not differ from that of analogous strata of the Moravian and Eastern Carpathians.

2. Elimination of the Kiczera and Krzywe 36 tuffs from further considerations results in rejuvenation of the upper part of the Krosno Fm. Accepting that – following Ślęzak *et al.* (1995b) – the lower part of the Dydnia Mbr, together with Bandrów and Dobrzanka tuffs, refers to NN3 zone (18.3 to 19.0 Ma), we obtain ages compatible with uncorrected age of the Bandrów Tuff (18.4 Ma) and extrapolated age of the Dobrzanka Tuff (18.6 Ma). Sedimentation of higher-situated beds (top of the Capor Mbr, middle and upper portion of the Dydnia Mbr, Leszczawka Mbr, Polyanytsya Mbr) could have occurred in the lower part of NN4 zone (Ślęzak *et al.*, 1995b). The presence of NN5 zone has not been documented; therefore, one can only accept a corrected age of the Krzywe 37 tuff (16.7 Ma).

Zonal affinities of the Menilite-Krosno Series members, according to the two options, are shown on Fig. 2.

EXAMINED SECTIONS

Eastern part of the Polish Carpathians

Real thickness relationships between the two facies of the Menilite-Krosno Series are shown on Fig. 3. Each column represents one or two neighbouring sections, from which ichthyofauna was collected. The latter was mainly confined to exposures of the Menilite Fm.; nevertheless, the Krosno Fm. was also taken into account to explain stratigraphic relationships and the importance of key horizons for palaeofacies reconstructions. Columns shown on Fig. 3 usually represent complete sections of MKS. In three cases (RR, W, MR-KS), the youngest strata of the Krosno Fm., irrelevant for the studied problem, were omitted except for giving the length of the missing sections. In two cases (T-D, H), in turn, few segments of one of the two formations were not drawn. The logs were assembled following the succession of tectonic units of the Carpathians, i.e. DU, SU, SSU, SKU, BPU, and their second-order structures (cf. Fig. 1).

On the right-hand side of each column, thick lines mark those segments of the Menilite-Krosno Series which were logged in detail and shown at a larger scale on synthetic and composite sections (Fig. 4). The succession of individual sections differs slightly from that on Fig. 3; section T-D is succeeded by an assemblage of columns arranged at a continuation of the studied line farther to the NE: L-HP, K-HB, BR-BH, i.e. representing the SE part of the area. These are succeeded by an assemblage of similarly arranged columns: H, B, BN-HT, BP, although representing the NW part of the studied region. Finally, columns illustrating development of the Menilite Fm. in the outer part of the basin have been drawn. On Fig. 4, different colours mark dominant lithological types of both formations, linking sometimes a few similarly developed lithologies into one unit; like, for instance, clayey-siliceous shales (mudstones) differing in fissility. On both figures, the base of each column marks the lower boundary of the Menilite Fm. in a given section.

All sections of the Menilite Fm., as well as sections: PS, WZ, MR-KS, T-D, L-HP, B, K and BR of the Krosno Fm. were reconstructed and logged by J. Kotlarczyk. Reconstruction of the remaining sections was based on data published by: Jucha (1969), Rajchel (1989) – at HT, and Wdowiarz (1948) – at BP.

To the left of each column on Fig. 4 the position and extent of the most important sampled exposures are shown (some of them are marked in detail on Fig. 6). In case of exposures situated far from a section, their projected position should be treated as approximate one, as marked by a dashed line.

Description of sections shown on Figs 3 and 4

1. Wisłok Wielki – WW. The section includes: (1) a few lower members of the Menilite Fm., called the “lower Menilite beds” or “sub-Cergowa beds”; (2) the Cergowa Member; (3) the “upper Menilite beds”; as well as the Krosno Fm. composed of: (4) “transitional” and “lower”, (5) “middle”, and (6) “upper Krosno beds” (*auct.*). The succession of beds can be traced in sections of the right and left (Cyłowa) tributaries of the Wisłok River at WW (Marginal Fold of DU). The sampled segment represents the transition between the Cergowa Mbr and “upper Menilite beds”, in-

cluding a sequence bearing the upper cluster of TLH layers. It is exposed in a forest road leading to Bukowsko.

2. Rudawka Rymanowska – RR. Section reconstructed along the Wisłok River includes the following units: (1) “sub-chert beds”; (2) cherts of the thinned Kotów Mbr; (3) the Cergowa Mbr, thinner than at WW; (4) the “upper Menilite beds”, 140 m thick, bearing TLH at the base; (5) the “transitional beds” (shales and sandstones of the Krosno facies intercalated by shales of the Menilite facies); and (6) complexes of the Krosno Fm. bearing different names. These beds build the imbricated SW limb of the Rudawka Rymanowska Fold. Fish assemblages were collected in the lower slice from the Kotów Chert Mbr (RR_{4, 4a}), and in the upper slice from the “upper Menilite beds” (RR₁₋₃). A. Jerzmańska did not manage to describe the assemblage from RR₀₃ exposure, while another assemblage, collected at a similar position from the sequence bearing a cluster of TLH of other exposures in the Wisłok River bed, was published by Bieñkowska (2004).

3. Równie – R. Section exposed in the right bank of the Jasiołka River is composed of: (1) a sequence of sub-chert beds; (2) the Kotów Mbr; (3) the Dynów Mbr; (4) the overlying sequence, ca. 110 m thick, of Menilite Fm. undivided into members; and (5) the lower part of “transitional beds”. Younger elements of the bed sequence from the same, SW limb of the Bóbrka Anticline, were logged (Jucha, 1969) in a more distant, western part of this limb. Fish assemblages were collected at exposures R₁, R₄, BB₁₁₈, and BB₁₀₄ situated in the SW limb, as well as at those from roadcuts in the NE limb of this anticline: RO₁, KL, and in the Jasiołka River bed – RO₂ (basal cherts).

4. Winnica – W. Section of the southern limb of the Potok Anticline includes strata exposed in the right-hand bank of the Jasiołka River (high escarpment) and in the higher-situated road, which belong to: (1) the Kotów Mbr, (2) Dynów Mbr, and (3) upper part of the undivided Menilite Fm., whereas other sections include: complexes (1) and (2) at BO, and (1), (2), and (3) at KR, as well as (4) “transitional” and “lower”, (5) “middle” with JLH and “upper Krosno beds”. A fish assemblage occurring in JLH was collected in Łapiguz brickyard at Sobniów (SO) near Jasło. Section SO (Fig. 4) is situated ca. 6 km to the west of Winnica section (Fig. 1).

5. Przysietnica – PS. A reconstructed section of the several times imbricated MKS is represented by exposures distributed along country roads on a hill that is situated north of the road at Przysietnica. The lower slice is composed of the (1) “sub-chert beds”, (2) Kotów Mbr, (3) Dynów Mbr, (4) lithologically differentiated sequences which are equivalent to the Rudawka and Borek Nowy members, and (5) the Šitbořice Mbr together with WLH and JLH horizons. The upper slice, in turn, is mainly composed of the last member and the lower sequence of the “Krosno transitional beds”, probably representing a fragment of the Jutna Mbr. The uppermost slice is built up of the Krosno Fm. only, subdivided by Jucha (1969) into three, not so distinct lithological complexes. Fish assemblages were collected from a dozen or so exposures of the Šitbořice Mbr.

6. Wujskie – WZ. This strongly tectonically reduced section represents MFm. within SSU, starting probably from TLH through JLH. Its strata belong mainly to the Šitbořice Mbr, including a well developed WLH in the middle part. A fragment of KFm which is in tectonic contact with MFm. in the eastern part of the exposure probably belongs to SKU.

7. Mrzygłód – MR, Końskie – KS. Sections of MKS located between these two localities, representing the SW limb of the Mrzygłód - Tyrawa Solna Anticline, display a comparable facies development, enabling for a construction of one, composite section. Partial sections are situated on the right and left banks of the San River at Mrzygłód, in a left-hand tributary of the San River at Jutna, and in streams flowing through Końskie. The lower portion of MFm. includes the Jamna Dolna, Kotów, Rudawka, Borek

Nowy (including cherts), and Kliwa members. The upper portion of MFm. displays interfingering of two facies: noncalcareous Menilite shales bear intercalations of calcareous varieties accompanied by calcareous Kliwa-Krosno-type sandstones. The lower part of this complex, ca. 100 m thick, probably comprises two different levels of JLH: within Menilite shales (the thickest limestone beds being ca. 1 m thick) on the right bank of the San River (MR₁), and within green and grey calcareous shales of the base of the Lopyanka Mbr (total thickness of limestone layers amounting to 30 cm) on the left bank (Jutna). The Lopyanka Mbr is here more than 400 m thick. It is composed of sandstones and shales of the Krosno facies which include three intercalations of Menilite shales, 20 to 60 m thick (MR₃). Another, higher-situated intercalation (30 m) with chert layers (MR₄) belongs to the Korzeniówka Mbr, and the overlying complex of thick-bedded sandstones of the Krosno facies represents the Jutna Mbr, ca. 300 m thick. Previous papers assigned the Lopyanka and Jutna members to the "lower Krosno beds", *partim* to the "transitional beds", whereas the Capor and Dydnia members overlying the Niebylec Mbr used to be included into the "middle" and "upper Krosno beds" (Koszarski & Szymakowska, 1961; Ślęzak *et al.*, 1995a). Introductory sampling of MFm. exposures provided either very rare assemblages (MR₁, KS₃) or solitary specimens of ichthyofauna.

8. Temeszów – T, Dobra – D. The column represents a composite section. The main section across MKS in the SW limb of the Witryłów Anticline extends between Temeszów and Krzywe (T₂ – T₄), whereas supplementary data are derived from Dobra (D) in the NW limb of this structure, where fish assemblages were collected. Another section extends between Dobra Góra (DG), Ratny (RT) and Siemowica (SE) exposures, and includes the lower part of MFm., which occurs in the SE limb of the Wara Anticline. This section is supplemented by exposures at Temeszów (T₁) and Obarzym (O₂). The Menilite Fm. comprises Jamna Dolna, Kotów, Dynów, and Rudawka members, being overlain by a ca. 100 m thick complex of the Kliwa-type sandstones bearing intercalations of green shales at the top. This complex represents either the Kliwa Mbr or a complex which is older than the Krępak Mbr. The higher part of this section, following a gap in exposures, contains calcareous Kliwa-Krosno-type sandstones and marly Menilite shales. The upper portion of the ca. 100-m-thick segment includes JLH, and 70 m above the latter and above T₂ exposure there occur thick-bedded Krosno sandstones, already representing the base of the Lopyanka Mbr. This member extends as high as exposure SE. The lower boundary of the Jutna Mbr cannot be distinguished due to the lack of the Korzeniówka Mbr. The upper part of the former is marked on the main section shortly below the Niebylec Mbr (cf. Fig. 3), which, in turn, is overlain by the Capor and Dydnia (including Dobrzanka Tuff Horizon) members. The section terminates by the Leszczawka (ca. 25 m thick) and Polyanysya (ca. 75 m thick) members.

9. Hłudno – H. In this section, MFm. builds the NE limb of the Wara Anticline which is refolded and thrust upon the Leszczawka-Nozdrzec Syncline. Reconstruction of stratigraphic succession in this area was a very difficult task. The section was reconstructed on the basis of numerous partial sections; and the synthetic section comprises segments which are separated by gaps, the size of which is hardly defineable or roughly estimated. Estimating the thickness of MFm. in the undisturbed SW limb of the Wara Anticline, situated at the same longitude, proved very helpful. For instance, the portion of MFm. located above JLH amounts to 400 m (Jucha, 1969), whereas the total thickness of MFm. approaches that at Temeszów. The reconstructed section includes: the Boryslav (H₁₃₂), Kotów (H₆), Dynów, Rudawka (H₅₋₁), and Borek Nowy (H₅₋₂) members. Approximately 80 m above JLH (H₁₁₉), there occur elements of the mixed Menilite-Krosno facies (H₇, H₁) which, however, do not deserve to be distinguished as the Lopyanka Mbr. The

higher-situated, ca. 150-m-thick segment of MFm. (H₂, HD₃, HDK₁, HD₁) comprises alternating sequences of either Kliwa-type sandstones or Menilite shales with frequent intercalations of thin-bedded sandstones. This segment can be compared to the peripheral zone of occurrence of the Błażowa Mbr. Detailed reconstruction of stratigraphic succession of the younger portion of MFm. has proved unsuccessful. This portion is most probably composed of a complex of the Kliwa-Krosno sandstones, including intercalations of thick-bedded Krosno sandstones at the top (Jutna Mbr?). In front of the imbricated, NE limb of the Wara Anticline, only the upper part, 300 m thick, of the Capor Mbr with the Dobrzanka Tuff Horizon does expose. The older portion of Kfm. is hidden under the overthrust (cf. Fig. 3).

10. Leszczawka – L, Huta – Poręby – HP. The section of MFm. was reconstructed on the basis of a transect across a left-hand tributary of the Stupnica River, near Bziany Hill. The section of Kfm., in turn, was constructed basing on a detailed geological map of the Leszczawka Syncline (Kotlarczyk, 1966). The MFm. includes the following members: Jamna Dolna, Kotów, Dynów, Rudawka, Borek Nowy, Krępak, and Kliwa, the last one bearing JLH at the top. The upper part of MFm. section is composed of alternating strata that represent Menilite, Krosno, and mixed facies. The presence of the reduced Korzeniówka Mbr, comprising the upper chert horizon (Fig. 4), makes it possible to subdivide the above sequence into the Lopyanka and poorly marked Jutna members. The Capor Mbr, overlying that of Niebylec, is up to 1,150 m thick, and contains in its upper part the Dobrzanka Tuff Horizon. The younger Leszczawka Mbr is 275 m thick in Huta-Poręby section, whereas the youngest Polyanysya Mbr is only a dozen or so metres thick. Fairly numerous fish assemblages were collected at exposures L and L₁.

11. Błażowa – B. The section of MFm. was established in a periclinal part of the Futoma Fold, between Futoma and Trzech Krzyży hill at Błażowa; whereas the section of Kfm. is exposed at the continuation of this section into the Harta Syncline at Błażowa. The lower segments of MFm. section (Fig. 6) are presented by better exposed partial sections at Kąkolówka (KK₁) – Siedliska Mbr, and Straszydle (S₁, S₂, S₃) – Kotów, Dynów, and – in part – Rudawka members. The Futoma (stratotype) and Borek Nowy (Bm) members are well developed in this section, whereas the upper part is occupied by the Błażowa Mbr (from B_a to B₆). Certain influence of the Krosno facies can be recognised in the upper part of MFm. in the form of calcareous Kliwa-Krosno sandstones. There also occur intercalations of green shales. Shales of the Niebylec Mbr at Piątkowa Polska bear the most fully developed Piątkowa Diatomite Horizon (stratotype), as well as the IV tuff level (Końskie Tuff Horizon). The most numerous fish assemblages were collected from the lower members (S₁, S₂), JLH (ŁŁ₁), Błażowa Mbr (B_a, B₄), and shortly from beneath the last one (B₁).

12. Borek Nowy – BN. This synthetic section of MFm. was constructed basing on exposures situated in the northern limb of the Czerwonki brachyantocline, namely: Borek Nowy (BN), Czerwonki (C), Przymiarki (P), Hermanowa (HE, HK), and Błażowa Dolna (BW), as well as on an unpublished map by J. Kotlarczyk (1999). A sequence of Kfm. lithological complexes at the Harta section, including Harta (HT) exposure (SW limb of the Bachórzec Anticline) is, in turn, based on Rajchel (1989). The section includes: Jamna Dolna, Kotów (P₁₋₃), Dynów (P₆, BW, C), Rudawka (P₄, HE), Futoma (BN₃₋₅, BE), Borek Nowy (HK), and Makłuczka members, as well as Przyłasek olistostrome, shortly below JLH. The upper, not sampled part of the section is composed of sandstones of the Błażowa Mbr, including intercalations of calcareous sandstones in the upper portion (Fig. 4). The Niebylec Mbr is overlain by strata of the Capor Mbr, ca. 675 m thick, with the Dobrzanka Tuff Horizon at the very top (Fig. 3). The most numerous fish assemblages were collected at P₄ and HT.

13. Krępak – K. This stratotype section of MFm., exposed in the eastern limb of the Brzuska Syncline, was established basing on exposures which are situated in road-cuts of the winding Przemysł – Sanok road, and in streams flowing both to the south (Korzeniówka Stream) and to the north (right-hand tributary of Korzeniówka Stream) of this road. It is this section, to which exposures of the Huta Brzuska, located 3.5 km away, were referred.

The base of this section includes well-developed Boryslav Mbr strata which replace in part the lower portion of the Kotów Mbr (KI₃) and, above the latter (HB₁), Dynów Mbr. Both the Rudawka Mbr (KIV₁) with TLH at the base (KIG), and Borek Nowy Mbr (KIV₂₋₃) are lithologically similar. Well-visible members include those of: Krępak (KIV₄₋₅); Kliwa; Huta Brzuska (KI₁, KI_{III}, HB₅, HB₆) with JLH at the base (KI); Lopyanka, and Korzeniówka (KII_h – KII) which bears the upper chert horizon. Numerous intercalations of the Kliwa-Krosno-type sandstones are to be noted in the latter.

The Krosno Formation is represented by the Niebylec Mbr which also includes the poorly developed Piątkowa Diatomite Horizon and the lower part of Capor Mbr. The most numerous fish assemblages were collected at exposures: KI₁, KII, KII₃, KIV₄₋₅ and HB₆.

14. Brzuska – BR. A section of MFm. in the NE limb of the Brzuska Syncline was constructed along the right-hand tributary of the Stupnica River (north of the road leading to Huta Brzuska), at Brzuska. Exposures of the section of a right-hand tributary of this river at Bachów, located 1 km to the north, were projected onto the Brzuska section. The log of KFm. is shown according to Kotlarczyk (1966). The section of MFm. comprises the same members as those occurring at Krępak, namely: Boryslav, Kotów (BR₂₂ in the lower part of this member), Dynów, Rudawka, Borek Nowy (BR₄₃ in the lower part of this member), Krępak (BR₃₉), Kliwa, and Huta Brzuska (BR₁₁, BR₃₄, BH₃) members. The Lopyanka Mbr is strongly reduced, being represented by isolated Krosno-type sandstone beds in the Bachów section, while the Korzeniówka Mbr (BR₁ – BR₁₀) is more lithologically homogeneous. Rocks of the Niebylec Mbr are overlain by the Capor Mbr bearing Dobrzanka Tuff Horizon in its upper part (Fig. 3). The reduced (?) Leszczawka Mbr and Polyanytsya Mbr terminate the section of KFm.

15. Babice Połanki – BP. A synthetic section of MFm., occurring in the NE limb of the Huta Drohobycka Syncline, was assembled in the Świnka Stream, a left-hand tributary of the San River, between Połanki and Dubiecko-Babice road, and supplemented by observations gathered in partial sections at Przedmieście Babickie (PB), Bachów – Zadworze (BZ), and more distant localities of Skopów (SK) and Średnia (SR). This section was compared with that of the lower part of MFm. which is exposed at Wola Węgierska (WE). A section of KFm. of the Świnka Stream (Fig. 3) is presented after Wdowiarz (1948).

16. Łodzinka – Ł, Jamna Dolna – J. A section of MFm. is exposed best in a stream flowing north of Bircza-Łodzinka road, at Łodzinka (Fig. 4). Fish-bearing exposures, in turn, are situated in a stream flowing south of this road. The lower part of the MFm. section is shown according to the sequence exposed at Jamna Dolna which is situated in the same tectonic structure, although 4 km more due south. The section is incomplete due to tectonic reduction of its upper segment; and its character is different from that observed at Krępak owing to the lack of sandstones. There occur Jamna Dolna, Kotów and Dynów members, as well as tectonically reduced and hardly discernible Rudawka, Borek Nowy, and Krępak members. These are overlain by a 35-m-thick complex of shales bearing chert layers, the lower part of which contains two clusters of laminated JLH limestones, ca. 10 m apart. The upper part of this complex, i.e. that situated above JHL, should be referred to the Huta Brzuska Mbr. The latter underlies not very thick (ca. 15 m) strata of the Lopyanka Mbr and the basal part of the

Korzeniówka Mbr. Rich ichthyofaunal assemblages were exploited from Jamna Dolna exposure only.

17. Książce – KN. A section of the Menilite Fm. is discontinuously exposed in the marginal slice of BPU, in a stream flowing SE of a forester's house. The lower part, not visible at present, was constructed basing on Gucik's (1988) data. This part represents the Kotów and Rudawka members. The Krosno Fm. was tectonically reduced.

A shale complex occurring above the olistostrome (Fig. 4) bears intercalations of green shales (KN₄) which can represent an equivalent of either Krępak or Makłuczka members. A large portion of the Menilite Fm. below JLH, obscured at present, is composed (according to Gucik, 1988) of brown Menilite shales, grey shales, and Kliwa sandstones. The latter can be related to the presence of the Kliwa Mbr, although the occurrence of grey shales can point to an early appearance of the Lopyanka Mbr. This member undoubtedly occurs shortly below and above JLH (KN₁), and is composed of typical lithologies. The top of the section exposes a thin sequence of Menilite shales bearing chert intercalations, probably representing the Korzeniówka Mbr. Contact zone between the Menilite Fm. and deposits of the overthrust slice is not exposed.

18. Dubnik – DU, Berendowice. The second section of the Menilite Fm. in the first marginal slice was constructed basing on exposures in a country road between Dubnik and Oliwna Góra Hill, i.e. 8 km south of the previous section. Data lacking from the lowermost part were supplied on the basis of a partial section near Berendowice (Fig. 1). The Menilite Fm. at Dubnik is also tectonically cut at the top; tectonic contacts occurring within the slice as well. Section at Berendowice exposes the Kotów, Dynów, and Rudawka members. Up the section, there occur: (1) calcareous shales of the Krosno type, (2) cherts, and (3) Menilite shales with thin-bedded sandstone intercalations. It is likely that they still belong to the Rudawka Mbr.

In the Dubnik section, the lower shale complex resembles the Makłuczka Mbr, probably with the Przyłasek olistostrome at the top (DU₄); although the lowermost, thick intercalation of green shales could also be an equivalent of the Krępak Mbr. The middle part of the section is composed of strata known from the Lopyanka Mbr, and its central portion (DU₃) comprises the lower cluster of JLH layers. The upper part, in turn, includes three different shale complexes: (1) brown siliceous-clayey shales with chert intercalations (DU₂), (2) green shales, and (3) brown shales bearing spherankerites (DU₁). The first complex is most probably an equivalent of the Korzeniówka Mbr; its bottom part comprising laminated layers of the JHL type. The second complex represents the Oliwna Góra Mbr.

Western part of the Polish Carpathians

Assigning the Choczniak (CH) and Krakowica (KW) sections to one of the main Carpathian tectonic units raises serious difficulties. According to Książkiewicz (1951; see also Nowak 1966), both sections represent the so-called Outer Flysch Unit which is situated north of SSU. Some authors, starting from Koszarski (1985), considered this unit a continuation of SKU. It was also suggested that the area comprising the Choczniak section belongs to SSU (Golonka 1979). One should also take into account a possibility that the Outer Flysch represents a lower digitation of SSU only. Farther to the west, it is this unit which builds the outermost element of the Carpathians. Given this uncertainty, both the discussed sections have not been assigned to any particular tectonic unit and are described separately. Detailed identifi-

cation of tectonic units is not necessary for the purpose of this study, since fish assemblages are derived from lower members of the Menilite Fm. which occur throughout all the units in question.

Description of sections shown on Fig. 4

1. Choczni \acute{a} – CH. The section is exposed on the right bank of the Kon \acute{o} wka Stream, dissected by a few gullies. There occur: sub-chert beds with intercalations glauconitic sandstones, Kot \acute{o} w and Dyn \acute{o} w members, and a complex of shales and thin-bedded sandstones which resemble those of the Rudawka Mbr (CH). In a side gully, south of CH exposure, one can find ca. 85-m-long exposure of weathered Menilite shales and thin-bedded sandstones, bearing intercalations of hornstones in the lower part.

2. Krakowica – KW (Inwałd). The area is obscured by tectonic outliers, regoliths, and vegetation, making reconstruction of the MKS section difficult. The described synthetic section is based on two partial sections: of the upper reach of a right-hand tributary of the Wieprz \acute{o} wka Stream, and of a right-hand gully of the Frydrych \acute{o} wka Stream, situated ca. 1 km to the north. Both these sections are probably situated within limbs of a syncline which is built up of the Krosno Fm. The Menilite Fm. at Krakowica is much more thinner (~45 m) than at Choczni \acute{a} , although distinctly tectonised, resulting in apparent shortening of the section. The following units can be distinguished: sub-chert beds, Kot \acute{o} w Mbr, Dyn \acute{o} w Mbr, and a complex of siliceous-clayey shales bearing TLH at the top. The higher part of the section includes shale complexes with intercalations of cherts and thick-bedded Kliwa-Krosno sandstones, sometimes of the Jawornik sandstone-type.

LITHOLOGY OF THE MENILITE-KROSNO SERIES

Analysis of the environment of ichthyofaunal taphocoenoses requires in-depth determination of lithology of the Menilite-Krosno Series, i.e. different types of rocks and their sequence. These will be presented on examples of a number of sampled sections.

For the purpose of this work, 18 exposures out of 75 studied have been chosen taking into account the following criteria, from which at least two should be fulfilled: (1) the exposure represents either stratotype or hypostratotype of a lithostratigraphic member; (2) ichthyofaunal assemblages were collected from marked layers; and (3) the exposure bears a boundary between ecological assemblages, or contains characteristic assemblages which helped to define stratotypes of ichthyofaunal zones and their boundaries. The last criterion resulted in choosing those exposures which represent SKU and SSU only.

The list of chosen exposures includes of course those, for which tables of respective fish assemblages collected from individual layers were constructed and will be presented in farther chapters.

Affiliation of the chosen exposures to lithostratigraphic members is shown on Fig. 5. In case of those few members, wherefrom infrequent fish assemblages were collected at individual exposures, their position is marked on Fig. 5 by dashed lines and italics.

All lithological types distinguished in the sections of exposures (Fig. 6) will be briefly characterised below.

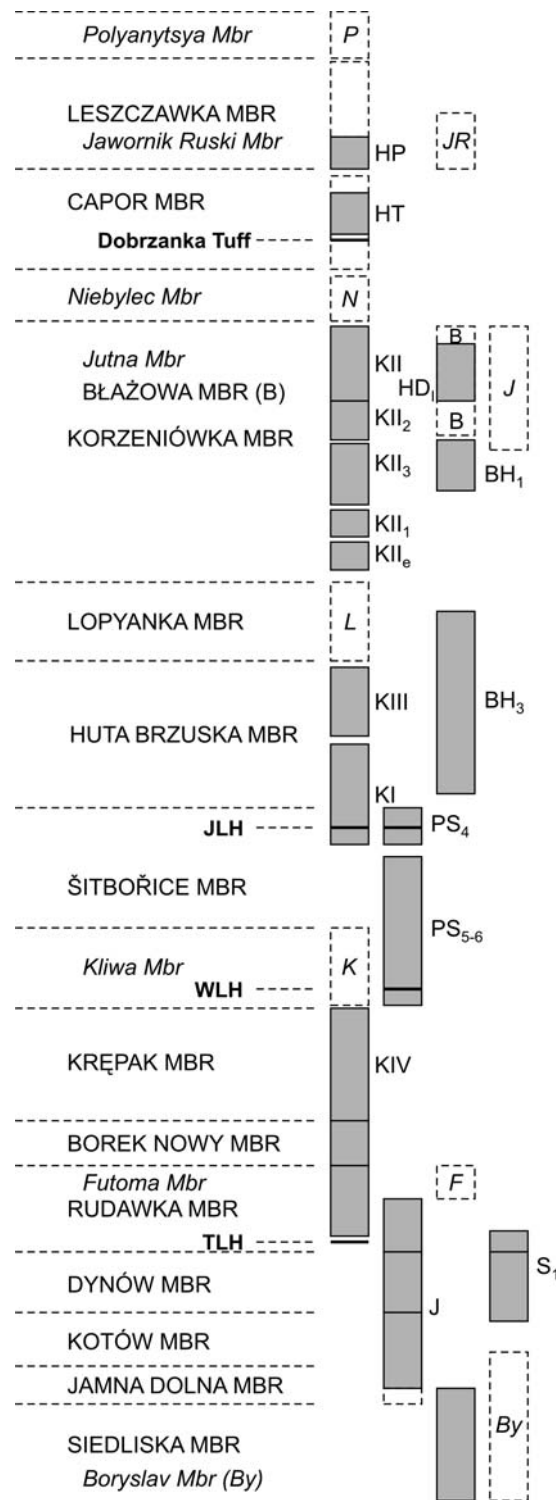


Fig. 5. Affiliation of exposures (columns accompanied by acronyms) shown on Fig. 6 to lithostratigraphic members. Dashed lines mark those members (columns bearing symbols of member names shown in italics) or their fragments which have not been taken into account in the set of selected detailed sections of exposures presented on Fig. 6

Each of the two facies, Menilite and Krosno, is typified by a set of different lithological types. General properties of the Menilite facies are as follows: (1) dark-brown or black colour of the majority of shales, diagenetic cherts, and some sandstones bearing a large proportion of muddy cement due to increased amount of organic matter; (2) bright, white, creamy, yellowish or beige colours of the majority of sandstones, hard marls, platy limestones, diatomites, and tuffs; (3) nearly complete lack of carbonates within shales and usually poorly-cemented sandstones; (4) predominance of pelitic rocks over psammitic ones; and (5) a marked proportion of free silica derived from diatoms and sponge spicules, resulting in frequently occurring silification of different rocks.

Properties of the Krosno facies, in turn, include: (1) bright, grey, blue-ash-grey colours of all rock types; (2) significant amount of muscovite; (3) ubiquitous presence of carbonates; and (4) large amount of psammitic rocks.

It is important to note that the Menilite facies includes lithological types showing properties of both facies. These are brown and black, strongly marly shales, and the Kliwa-type sandstones bearing a minor admixture of mica and poorly-calcareous cement. Different types of rocks occurring in MFm. have been described in numerous papers (cf. Kotlarczyk & Leśniak, 1990). The following characteristics concern only those rocks which compose sections of the sampled exposures (see Figs 5, 6).

Menilite facies

1. Leaf-like (clayey-siliceous) and scale-like shales (mudstones) differ from each other by the percentage of principal components as well as thickness and shape of weathered rock fragments, i.e., resp. flakes and plates, up to two centimeters thick, which thin out in different directions. These rocks occur most frequently.

2. Platy and sheet-like (siliceous-clayey) shales tend to disintegrate along parallel surfaces into 2 cm or 1–2 mm thick fragments, respectively. These shales are frequently interlaminated by quartz silt which also occurs in dispersed form. The shales are usually confined to the lower part of MFm.

3. Lump-like shales (mudstones) disintegrate when weathered along conchoidal surfaces. This variety is mainly associated with the upper part of MFm.

4. Shales (mudstones) of crude and sliver-like fissility disintegrate into irregular fragments or – due to cleavage – elongated chunks that resemble slivers of wood. The shales are abundant in the Nowosiółki Dydyńskie Mbr and in the upper part of MFm. in SKU. In SU, in turn, they appear above TLH.

5. Marly shales tend to reveal scale- or lump-like fissility. These rocks occur rarely in those parts of the basin which show either traces of the Krosno facies or interfingering of the two facies. The shales are mainly confined to the Lopyanka, Jutna, and Niebylec members.

6. Green and greenish-grey, clayey-siliceous shales tend to reveal leaf-like fissility. They occur sporadically in different parts of the MFm. section, particularly in the Śit-

bořice and Křepak members, subordinately in the Kliwa and Makłuczka members.

7. Grey, clayey-siliceous, mica-free and usually noncalcareous shales show leaf- or scale-like fissility. Thin interlayers subordinately occur in the Korzeniówka and Leszczawka members, whereas calcareous varieties are to be found close to JLH in SSU.

8. Hard siliceous marls are usually thin-bedded, laminated or graded, light-brown, beige when weathered. Marl layers, alternating with very thin beds of marly shales, build the Dynów Mbr, the upper part of which contains in places flint concretions. When decalcified, porous rocks of siliceous framework are formed, and can easily be mistaken for diatomites.

9. Hard marls, thin and rarely medium-bedded, massive, showing either creamy-whitish or like above colours, sometimes siliceous and bearing flint concretions, occur in the Dynów and Jawornik members.

10. Brown marls of crude fissility, yellow, creamy or white when weathered, are in places intercalated by a few millimetres thick sets of fine laminae which bear abundant detritus of *Planorbella*. This variety occurs mainly in the Siedliska Mbr.

11. Diatomaceous rocks of light-brown, beige and creamy colour are mainly represented by diatomaceous mudstones (showing fissility comparable to that of Menilite shales), rarely diatomites, and in exceptional cases tuffodiatomites. Laminated varieties of these rocks occur in the Futoma Mbr along with non-laminated ones. The latter, however, are usually found in the Leszczawka Mbr. Pure diatomites frequently become silicified; some layers turn during early diagenesis into either cherts or porcelanites. Detailed characteristics of these rocks can be found, i.a. in Kotlarczyk (1966) or Kotlarczyk *et al.* (1986, 1991).

12. Brittle, light-brown, brown and black glassy cherts build either a few millimetres thick laminae or one to a dozen or so centimetres thick layers. In some cases, diagenetic processes were not completed, and cleavage surfaces of cherts are lustreless. Individual chert layers are separated by brown silicified shales of leaf-like fissility and variable thickness. A continuous sequence of cherts is to be found in the Kotów Mbr, while single layers or their clusters appear in the Rudawka, Borek Nowy, Korzeniówka (Upper Chert Horizon) and Leszczawka members.

13. White and beige porcelanites, lustreless and relatively light, build isolated thin layers, a few millimetres or a few centimetres, rarely a dozen or so centimetres thick. These occur mainly within diatomaceous beds of the Futoma and Leszczawka members, being sometimes associated with pyroclastic strata in the latter member. Dark-beige varieties appear in the Kotów and Rudawka members.

Psammitic rocks build numerous varieties and types (cf. Żgiet, 1963a ; Kotlarczyk, 1966, 1976a; Kotlarczyk & Leśniak, 1990), the common feature of which is a very large amount of quartz (quartzarenites) accompanied by minor percentage of clayey or siliceous cement and the absence of mica. These rocks are poor in sole marks (load-casts, drag marks, and deltooidal ones).

14. Ripple-cross laminated sandstones are thin-bedded, fine-grained, and interlaminated with brown silt which un-

derlines, i.a. ubiquitous occurrence of ripplemarks. Some sandstone beds, particularly in the Rudawka Mbr, originated due to traction currents (contourites, tractionites; cf. Dżułyński & Kotlarczyk, 1962; Unrug, 1980), while other beds represent T_{cd} Bouma members.

15. Medium- and thick-bedded (up to 6 m), vari-grained quartzarenites are composed of grains up to granule and gravel size. Top parts of beds frequently comprise large clasts of Menilite shales, and laminae build up of brown silt. In places, large-scale cross bedding occurs within the beds. These sandstones originated due to grainflows and fluxoturbiditic currents, and are typical Kliwa sandstones which occur within the Kliwa and Błazowa members, and in the inner part of SKU also within the Rudawka Mbr.

16. The Kliwa-Krosno-type sandstones (i.a. at Vama in Bukovina, Romania; Paul, 1876) represent that sedimentary environment of MFm. in which influences of the Krosno facies mark their appearance. The Kliwa sandstones tend to become poorly marly and their grain composition becomes enriched in muscovite. Sandstone varieties bearing a minor amount of both components were distinguished as the Magierów sandstones by Kotlarczyk and Leśniak (1990).

17. Greywacke-like sandstones and massive mudstones, brown or black-grey, bearing unsorted grains of variable size (quartz, feldspars, muscovite, sometimes glaucony, numerous small-scale lithoclasts of Carpathian and exotic rocks, including metamorphic and sedimentary ones). The amount of muddy cement is considerable, sometimes very high, resulting in a sequence of different rocks that range from sandstones (e.g., Jawornik Ruski Sandstones) to sandy mudstones. These rocks originated due to slow, mud-sandy cohesive flows (Kotlarczyk, 1966, p.31; Leszczyński, 1987). They occur more frequently within the Siedliska, Huta Brzuska and Korzeniówka members, and are principal components of the Jawornik Ruski Mbr.

18. Greywacke-like conglomerates and vari-grained sandstones, brown-grey or brown-green, build beds of variable thickness. These rocks are usually calcareous, compact, and bear abundant glaucony, along with frequent clasts of Carpathian and exotic rocks, as well as detritus or entire shells of molluscs. Structures typical of turbidites are common. The rocks are characteristic for the Siedliska Mbr, and calcareous sandstones with glaucony and bearing ripple-mark structures build thin interlayers in the Dynów Mbr.

Aleurites are ubiquitous in MKS, usually forming single laminae within shales and diatomites and building upper parts of sandstone beds, instead of separate layers. More abundant proportion of silt accompanied by clays is observed in commonly occurring mudstones.

19. Light-grey, quartzose, thin-bedded, noncalcareous siltstones occur within the Rudawka and Leszczawka members.

20. Chaotic deposits are represented by submarine slumps and olistostromes. These structures comprise distorted, bent, sometimes rolled-over fragments of sandstone, shale, siliceous marl, chert, diatomaceous siltstone, and other beds. The matrix is composed of sandy mud or does not occur at all. The thickness of such deposits ranges from a few metres to several tens of metres (fragments of the Leszczawka Mbr, Przylasek olistostrome, Popiele olistostrome).

Single slumped packets of siliceous marls (olistoliths) may resemble normal elements of the sequences of either Rudawka or Borek Nowy members.

Krosno facies

1. Ash-grey, clayey-marly, sometimes silty shales bearing fine flakes of muscovite. In places, they represent a single T_e member preceded sometimes by a silty lamina (T_{de}), although they usually build the uppermost member of the Bouma sequence which cannot be discriminated from clayey hemipelagic sediments.

2. Convolute, thin-bedded, ash-grey, strongly calcareous and mica-rich, typically turbiditic sandstones.

3. Medium- and thick-bedded, fine- to coarse-grained, ash-grey or bluish-grey, calcareous sandstones.

These principal, and also other types of rocks, all of them turbiditic, have been described many times (cf. Dżułyński & Ślącza, 1959; Koszarski & Żytko, 1961; Jucha & Kotlarczyk, 1966). These rocks occur throughout the Krosno Formation, as well as in a few members of the Menilite Formation, namely: Papin, Cergowa, Lopyanka, and Jutna members.

Marker horizons

1. Finely laminated, whitish-creamy, sometimes beige-brown, platy limestones tend to build layers which range in thickness between a few millimetres to a few centimetres. Darker laminae bear an admixture of clay minerals. Apart from laminated rocks, there occur alternating, usually thicker layers of non-laminated limestones or bearing single laminae only. It is this variety, the upper cluster of limestone layers of JLH is composed of. Both varieties within JLH and TLH are commonly stuck together. Particularly thick and slightly marly beds, up to 70 cm thick, occur in TJH. Laminated limestones represent pelagic (or hemipelagic) sediments, while thick beds of non-laminated limestones may belong to turbiditic unifites. Certain types of dark-coloured limestones like, for instance, those in WLH, tend to weather easily and become brittle, porous and yellow. More detailed descriptions are comprised in papers by Koszarski and Żytko (1961), Jucha (1969), Haczewski (1989) and Bubik (1992).

2. Tuffs, tuffites and bentonites. Pyroclastic rocks of vitroclastic or ash structure are ash-grey, frequently of greenish hue, or white-yellow. Certain, slightly silicified varieties tend to disintegrate into lumps. Tuffites are sometimes finely laminated. Individual beds are from a few centimetres to a few metres thick. Bentonites, in turn, frequently build single layers that are composed of soft rocks, green or yellow-green, which easily disintegrate in water. Those bentonites which build upper members of tuffaceous rhythms are silicified, grey-greenish, and tend to disintegrate into angular fragments.

SEDIMENTATION OF THE MENILITE FORMATION

Any reconstruction of the environment of ichthyofaunal taphocoenoses in a sedimentary basin requires careful analysis of depositional processes. The hitherto-conducted studies in SU and DU are not sufficient enough to explain such processes in detail, in contrast to SKU and SSU which have been in-depth investigated. Beneath, we shall repeat the results of those previous studies which helped to construct a model of deposition of the lower part of MFm. within SKU (Kotlarczyk & Leśniak, 1990; Kotlarczyk, 1991).

The described fragment of the Tethys basin consisted in Oligocene times of the following elements: (1) shelf, (2) continental slope of the East-European Platform, (3) continental rise, (4) bottom of the Skole Trough, subdivided in its eastern part into (4a) narrow, outer furrow of BPU, and (4b) broad furrow of SKU, (5) submarine rise (ridge) accompanied by an island arc (Sanok "cordillera") which separated SKU from (6) a broad trough of SU-DU (Fig. 7). Sediments deposited upon this ridge build now SSU (in the western part of the Polish Carpathians, near Wadowice – see Fig. 1, sediments of SSU were deposited on the bottom of the outer furrow of the Menilite basin). The southern slope of the SU-DU Trough and the entire basin was represented by the intrabasinal ridge – remnants of the Silesian "cordillera". Judging from ichthyofaunal composition, the initial minimum depth of the basin was either 1,500 m or 2,500 m.

The MFm. sediments in SKU and BPU are represented exclusively by deposits of both the slopes, continental rise, and basin bottom. Shelf sediments have only been preserved as olistoliths and clasts. These must have been derived in gross part from a carbonate platform surrounded by reefs. The continental slope was probably cut by fault zones which led to disintegration of rocks and supplied detrital material to olistostroms, debrites, and turbidity currents (Dżużyński & Kotlarczyk, 1988). Mobilization of gravitational mass movements affecting material deposited close to the shelf

break and upon slope was triggered by earthquakes, tsunamis, or due to overloading of the slope. Density bottom currents flowing down the slope facilitated tractional transport, leading to deposition of tractionites.

However, detrital material of variable size used to be supplied into the basin mainly by channels of elongated submarine fans. The smallest grains could have also been supplied in clouds of suspended load, detached from the slope and prograding towards the trough's axis along the pycnocline surface (cf. Stanley, 1983); within muddy turbidites; from nepheloidal layer; and owing to aeolian transport. The amount of biogenic material, originating in the euphotic zone, is difficult to estimate within pelitic sediments except for such deposits as the coccolith Jasło, Tylawa, and Wujskie limestones.

Senkovsky *et al.* (2004) link the origin of black shales of the Menilite Fm., rich in organic matter, with permanent activity of upwelling along continental slope of the northern Tethys basin. This upwelling is supposed to have led to the formation of the oxygen-minimum layer at depths between ca. 500 and 1,500 m, providing anaerobic conditions also within sediments deposited at these depths. The presented model (*op. cit.*, fig. 42) is, however, hardly compatible with the presence of deep-water fishes which dwelled, except for a short episode, this zone during deposition of the Menilite Fm.

Field examination made it possible to conclude that (1) sandy lithosomes composed of the Kliwa-type sandstones are elongated in shape, and (2) maintain comparable position on the bottom, irrespectively of age. Orientation of these lithosomes is compatible with that of the axes of swells of intervening members that are composed of pelitic-aleuritic facies, such as the Kotów, Dynów, Rudawka, and Borek Nowy members. These observations enable one to distinguish four submarine fans in the study area: Dębica SF, Rzeszów SF, Łańcut SF, and Przemyśl SF (Fig. 8). The fans are up to a dozen or so kilometres wide, and – without taking into account folding-induced shortening – up to 75 km long (Kotlarczyk & Leśniak, 1990). These fans com-

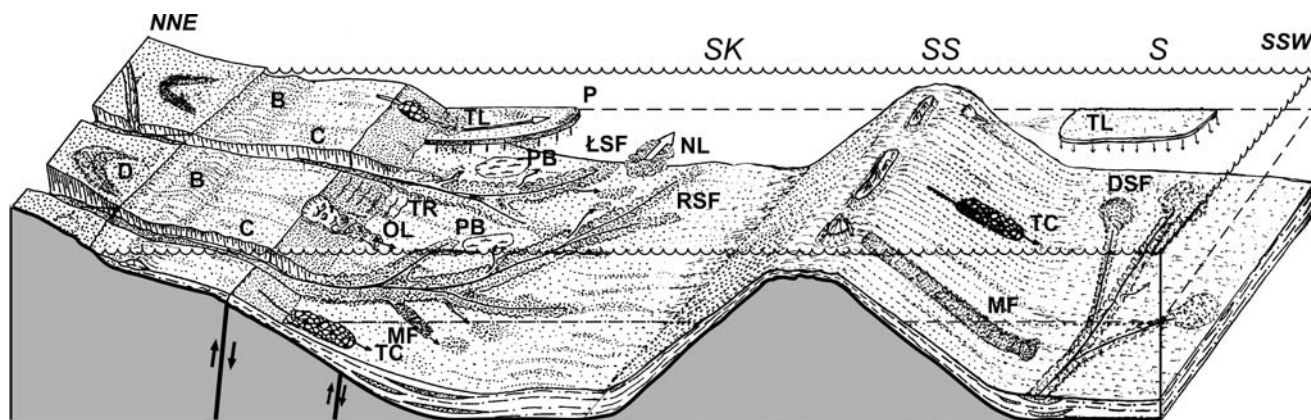


Fig. 7. A model of deposition of Menilite facies sediments in the basin of the eastern portion of the Polish Carpathians (based on Kotlarczyk, 1991a; supplemented). Symbols: SK – Skole Trough; SS – Subsilesian High (Ridge) including Sanok Cordillera; S – Silesian Trough; C – submarine canyon; LSF – Łańcut submarine fan; RSF – Rzeszów submarine fan; DSF – Dębica submarine fan; PB – perched basin; D – aeolian dunes; B – barrier reef; OL – olistostrome; TC – turbidity current; MF – cohesive mudflow; TR – tractionites; NL – nepheloidal layer; P – pycnocline, TL – broken layer of suspended load

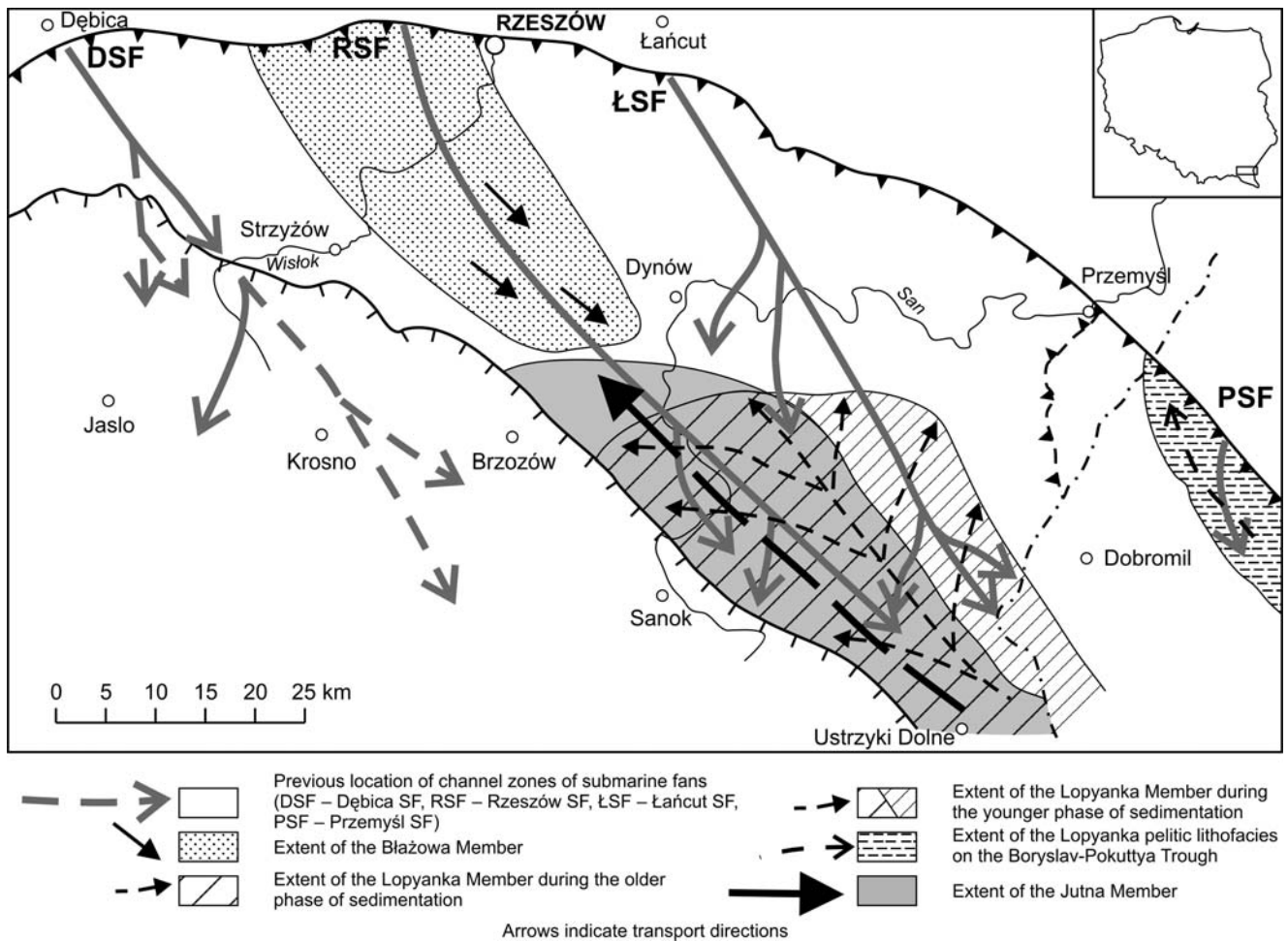


Fig. 8. Development of submarine fans in the Skole Trough during deposition of younger MFm. members. Outline of the trough shown before sigmoidal bending of the Carpathians near Przemyśl

prise structures typical of the channel facies, like: large-scale cross bedding, amalgamated beds, erosional furrows, as well as sediments of cohesive, debris, and grain flows. The Dębica and Rzeszów submarine fans include turbiditic conglomerates and sandstones of the Siedliska Mbr, and beds of the Kliwa-type sandstones which occur in lower parts of the main fan and its side distributary channels. The above-mentioned members composed of finer fractions allow one to suppose that also fines must have been transported through distributary channels of submarine fans. The material was transported above the levées (particularly left-hand side, lower ones) and filled inter-channel zones. The same was also applied to biogenic material which was originally deposited upon shelf, sometimes close to estuaries, like calcareous coccolith muds that build the Dynów Mbr, and diatom muds that compose the Futoma Mbr. This mechanism explains well the presence of brackish or even fresh-water taxa of the two groups of organisms (Krhovský 1981; Kotlarczyk & Kaczmarek, 1987), as well as the finding of a scale of a fresh-water fish *Barbus* sp. in the Dynów Mbr.

The longest distribution of the Kliwa-type quartzarenites, lasting until the end of deposition of MFm., characterised the Rzeszów channel (Błażowa Mbr). This northern

fan became then considerably shortened (Fig. 8), since the SE part of the basin bottom started to be filled with sandstone-dominated flysch of the Krosno facies. The lobes of this fan, supplying material from the SE, originated first in the axial part of the basin and then expanded towards the NE, upon continental rise, i.e. up to the Brzuska Syncline. The lobe's head reached as far north as the Brzuska-Dydnia line. The Lopyanka Mbr was deposited at that time. Somewhat earlier, pelitic sediments of the Krosno facies reached Książce area through the BPU furrow.

The second phase of expansion of the Krosno facies fan took place after distribution of this material had terminated and the Lopyanka Mbr strata had become covered by pelitic sediments of the Korzeniówka Mbr. It was this phase when fan lobes infilled the narrow, axial part of the SKU Trough and reached farther north. Near Hłudno, sediments of this lobe became alternated with those of lobe sediments of the Rzeszów fan. Sediments of the SE fan compose the Jutna Mbr.

Deposition in the innermost part of SKU, proceeding upon a submarine rise, took place outside the extent of lobes of both the northern and south-eastern fans. Only pelitic sediments did accumulate in this zone.

As far as SU is concerned, deposition of MFm. upon the

Dynów Marl Mbr proceeded in a different way. The formation is mainly composed of mudstones and shales interbedded with rare layers of cherts and thin- or medium-bedded, noncalcareous sandstones. Judging from geological maps of sheets Jedlicze and Rymanów, the thick-bedded Kliwa sandstones occur in the outermost, northern part of SU at Łączki Jagiellońskie (Szymakowska & Wójcik, 1992), Korczyn (Jucha, 1969), Trześniów (Wdowiarz *et al.*, 1991), and in the Wrocanka Fold, SSE of Jasło. These sandstones are also exposed at Rudawka Rymanowska, occupying the position of the Boryslav sandstones. It is worth to note that Jucha (1969) distinguished in MFm. an additional, narrow zone of increased sand content between Brzostek and Łączki Jagiellońskie (the so-called Gogołów-type of the Menilite Series, i.e. shale-sandstone facies of Jucha and Krach, 1962), in which common components are “clayey sandstones”, rarely “pebbly mudstones” with exotic rocks and rich molluscan fauna, that represent cohesive sand-muddy flows. At several places of this zone, the base of MFm. includes the Siedliska conglomerates (see also Szymakowska & Wójcik, 1992). The origin of increased proportion of clastic material used to be associated with the presence of the emerged “Sanok cordillera” (Jucha & Krach, 1962). However, the provenance of these rocks, including thick-bedded Kliwa sandstones, can be explained in a different way. All the above-listed sites form a narrow zone that extends NE–SW at a continuation of the Dębica fan (Fig. 8). Given that, one can assume that a submarine ridge separating the Skole and Silesian troughs must have been lowered in this area, forming a gate between Brzostek and Łączki Jagiellońskie. Clastic material of the Dębica fan was transported through this gate into the Silesian-Dukla Trough. Thick-bedded sandstones and cohesive flows which mark channel zones of the fan approached in the first, “sub-chert” phase as far as Rudawka Rymanowska, and in the following, “supra-chert” phase their extent reached the latitude of Krosno only. According to this hypothesis, thin- and medium-bedded turbiditic sandstones and mudstones (unifites) must have been deposited all over the discussed area of SU, i.e. also beyond the extent of channel zones of lobes of the lower fan. Similar reasoning should also be applied when explaining the origin of both the coccolith Jawornik Marl (i.e. sub-Cergowa Marl), which build much more thicker layers than those of the Dynów Marl and resemble unifites (Ślącza, 1990), and massive marly limestones which occur in the Tylawa Limestone Horizon. Biogenic components of these rocks would have been derived from a carbonate platform situated on the northern basin margin, and distributed via the Dębica fan.

From the very beginning, the activity of the Dębica fan (or another one situated farther to the west) was hampered several times in the innermost part of the Menilite basin: first during deposition of the Papin Mbr, then the Cergowa Mbr, and finally during sedimentation of the “upper Menilite beds”, due to expansion of fans composed of sediments of the Krosno facies. These fans were supplied from sources situated in the SE and, sometimes, in the NW (Ślącza & Unrug, 1976). Finally, deposition of the Menilite Fm. within the SU-DU Trough became completely replaced by sediments of the Krosno facies, which were shed from the SE

and WNW (Dzudyński & Ślącza, 1959). Basin infilling proceeded through expansion of several submarine fans (Wendorff, 1979, 1986a, 1986b).

Likewise, very quick infilling of the SKU Trough occurred in a phase that succeeded deposition of the Niebylec Mbr. At the same time, in the Eastern Carpathians, deposition of the Menilite facies alternated with that of the Krosno facies in the marginal part of SKU and in BPU (“upper Menilite beds”).

In the study area, the Menilite facies marked its appearance for the last time in the basin in the Leszczawka Mbr, during temporary slowing down of flysch deposition of the Krosno facies. The SKU Trough was then largely infilled by MKS sediments, the thickness of which ranged, after compaction, between 1,600 m to ca. 2,200 m in the axial zone.

Diatomaceous rocks bearing a large proportion of fresh-water diatoms (Kaczmarek & Kotlarczyk, 1979) are usually represented by massive mudflows. It is at the base of the member only, where beds tend to reveal poorly developed lamination. Isolated samples include either exclusively qualitatively poor assemblages of fresh-water taxa, or similar assemblages bearing an admixture of marine taxa. This points to migration of diatom material from the littoral zone through successive depth intervals to the basin bottom, which was then situated at shallower depths of the order of a few hundred metres (cf. further comments regarding basin bathymetry).

The presence of sand-muddy cohesive flows and thick-bedded Kliwa-type sandstones within the Leszczawka Mbr and, first of all, Jawornik Ruski Mbr points to a possibility that both these members originated due to activity of a submarine fan, whose channel could have supplied detrital and biogenic material, typical of MFm. (cf. Kotlarczyk, 1966), from the northern basin margin.

The most complete development of both members proceeded between the channels of the Rzeszów and Łańcut fans. Formation of a new fan after a long break in sediment delivery from the northern land and upon fans that build KFm. need not had to be related with the former-existing fans, although it cannot be excluded that the material was transported through the Łańcut fan’s canyon. An alternative explanation is that all types of material were shed from the shelf break directly along the continental slope, down to an elevated level of the continental rise.

The Leszczawka Mbr includes an olistostrome (Kotlarczyk, 1983) which is composed of large blocks, and earlier diagenised and even silicified at places diatomaceous mudflow sediments. These deposits indicate that the member must have been formed at the base of an inclined surface of either submarine fan or continental slope.

SEDIMENTARY ENVIRONMENT OF ICHTHYOFAUNAL TAPHOCOENOSSES

Isolated fragments of fish skeletons and scales can be found in nearly all varieties of MFm. rocks and thin-bedded sandstones of KFm., while entire skeletons or their fragments are confined exclusively to dark pelitic rocks, usually

more or less distinctly laminated, and to pelagic limestones showing brown-coloured lamination. Fish assemblages derived from light-coloured mudstones of the Krosno Fm. have been found within brown shales or in dark-beige laminae, whose colour markedly differs from that of the Krosno mudstones (cf. section HT on Fig. 6). In all these cases, fossils occur on the surfaces of laminae. The described sediments represent E.2.2, E.2.1 and G.1.2 facies of Pickering *et al.* (1986).

Fish skeletons are frequently met on those surfaces which separate different episodes of deposition, i.e. at the top or bottom of clay and mudstone strata of different types, as well as bedded limestones, cherts, and even sandstones. In such cases, the skeleton is associated with one type of sediment, and its imprint with another type. It is probable, although not sufficiently documented, that those skeletons which occur below sediments of a single depositional event are closely linked with hemipelagic sediments of G.2.1 facies which separate this episode from the preceding one.

Separation of the terminal member of the Bouma sequence, T_e, or sediments of diluted turbidity current, and even pelitic sediment delivered into the basin by another way in one depositional event (e.g., mudflow) from inorganic hemipelagic sediments originated, for instance, from a layer of detached suspended load or nepheloidal layer, is very difficult and even impossible during routine fish exploitation. Fossil fish reveal hardly any relationship with transport by turbidity currents. This is apparently indicated by the lack of observed current-controlled orientation of elongated fish bodies, as well as the occurrence of skeletons within one mud layer, although at different levels; a feature pointing to long-lasting burial and hemipelagic type of deposition. An important example is fish occurrence in banded, brown-green shales that show leaf-like, scale-like, and even conchoidal fissility (facies E1.2). These must have been deposited on a submarine ridge of SSU, where no traces of turbidity currents were found. Within these hemipelagic muds, fish tend to occupy different positions within sections of each brown layer.

In some places, fish skeletons appear within thick shale (mudstone) beds of crude, scale- or lump-like fissility, of turbiditic or flow origin. In such cases we are usually confronted with a bed composed of several depositional events, and the occurrence of fish is confined to the surfaces separating these events, i.e. single laminae of hemipelagic mud.

It cannot be excluded that in some cases the fish have been brought together with the material of a turbidity current or a flow. The latter case appears to be supported by rarely observed (E. Świdnicka), abnormal arrangement of skeleton fragments, i.e. across sedimentary surface of the layer.

The hitherto-gathered experience enables one to put forward an hypothesis that relocation of dead fish by mudflows must have played a negligible role in post-mortem transport. However, floating of these fish within mud turbidity currents and their deposition before the final sedimentation remains an open question.

COMPOSITION OF ICHTHYOFAUNA OF THE COLLECTION HOUSED AT THE DEPARTMENT OF PALAEOZOOLOGY, INSTITUTE OF ZOOLOGY, UNIVERSITY OF WROCLAW

The collection of fossil fish housed at the Department of Palaeozoology, Institute of Zoology of the University of Wrocław, comprises ca. 13,000 specimens, including ca. 12,930 specimens of Teleostei, and ca. 70 specimens of Chondrichthyes. The subject of this work is a set numbering 12,752 specimens, from which 10,705 (ca. 84 %) have been determined by A. Jerzmańska or her collaborators to the rank of either species or genus. Some of the specimens determined to the genus rank bear generalized names, whereas the term *species* includes sometimes a group of unidentified taxa. 1,105 specimens (ca. 8.7%) have been assigned to families, 408 specimens (ca. 3.2%) to orders, and 82 specimens (ca. 0.6 %) to other, higher-ranking systematic units (subclasses, suborders, subfamilies). For 452 specimens (3.5%), no taxonomic position rank has been established, whereas for a certain number of specimens distinguished within families, suborders, and orders A. Jerzmańska determined new types, called by informal names only: Bathylagidae, of type (Melania); Myctophidae, of type (Giant II); Sternoptychidae, of type (xz); Stromateidae, of type (Giant III); Salmoniformes (?), of type (xx); Perciformes, of type (à la, à la). Informal names of the taxa (given in brackets) as well as taxa of only inferred position in the classification scheme have been marked by asterisks (*).

The list of taxa presented in this chapter reflects the state of elaboration of ichthyofauna up to 1994. In 1998, introductory works aiming at detailed osteological description began. Future studies will include a revision of types determined on the basis of currently made revisions of holotypes housed at other collections of the world. It cannot be excluded that new descriptions will enable for a transfer of some forms into different families and orders.

The collection bears a systematic catalogue, Coll Fish-Carpath ZPaWr, prepared in the programme ACCESS 2002. The catalogue includes 61 species, 75 genera, and ca. 60 unidentified taxa that belong to 57 families and 21 orders of Teleostei, as well as 3 genera belonging to 3 families and 2 orders of Chondrichthyes. It comprises 15 holotypes and designated paratypes. The catalogue is of great scientific value, documenting palaeobiostratigraphical studies conducted on ichthyofaunal assemblages described from the Menilite-Krosno series of the Polish Carpathians.

The lists of taxa collected in the Polish Carpathians in the years 1954–2003 have been currently published in biostratigraphical and statistical papers, as well as in geological guidebooks. The complete lists of taxa have been published by Kotlarczyk (1985), and Jerzmańska and Kotlarczyk (1988).

The collection includes as well a number of taxa from the Polish Carpathians that have not been mentioned in previous lists or publications: *Acanthocybium* sp.; *Ammodytes* sp.; *Apostasis* sp.; *Barbus* sp.; *Bathyprius* sp.; *Bregmaceros* sp.; *Caprovesposus* sp.; *Caranx petrodavae* Simionescu 1905; *Caranx* sp.; *Centriscus* sp. A; *Diaphus* sp.; *Forcipi-*

Table 3

State of preservation and the number of specimens within individual categories

State of preservation	Number of specimens	%
Complete skeletons	3,314	25.5
Incomplete skeletons (the head part of the spine)	2,720	20.9
Incomplete skeletons (the caudal part of the spine)	1,727	13.3
Middle parts of the spine	1,935	14.9
Isolated heads	1,583	12.1
Minor parts of the skeleton, isolated bones, and fin skeletons	1,471	11.3
Teeth, sucking discs, otoliths, scales	250	1.9
TOTAL	13,000	100%

ger sp.; *Holosteus mariae* (Menner 1948); *Holosteus* sp.; *Idrissia* sp.; *Mugil* sp.; *Nessorhamphus* sp.; *Oligobalistes* sp.; *Oligolactoria bubiki* Tyler et Gregorova 1991; *Onobrosomus* sp.; *Palaeogadus carpathicus* Świdnicki 1991; *Palaeogadus distinctus* Świdnicki 1990; *Palaeogadus intergerinus* Daniltshenko 1947; *Palaeomolva monstrata* Fedotov 1974; *Palimphytes lanceolata* (Simionescu 1905); *Paraberyx bachoviensis* Jerzmańska 1975; *Paraberyx* sp.; *Parahollardia*? sp.; *Parasteindachmeria oligocaenica* Świdnicki 1990; *Pinichthys* sp.; *Polyipnus* cf. *anteasteroides* Ciobanu 1977; *Polyipnus* sp.; *Priacanthus* sp.; *Propercarina* sp.; *Properca* sp.; *Propteridium* sp.; *Protomyctophum* sp.; *Psenicubiceps* sp.; *Scorpaena* sp.; *Scorpaenoides popovicii* Priem 1899; *Serranus* sp.; *Solenorhynchus* sp.; *Sphyræna* sp.; *Syngnathus* sp. A; *Syngnathus* sp. B; *Vinciguerria merklini* Daniltshenko 1946; and *Vinciguerria talgiensis* Daniltshenko 1946.

Specimens comprised in the collection have been described at different levels of precision. Nearly 30% of specimens bear full description and diagnosis. These specimens have been mainly determined up to the species, rarely genus level, and most of them have already been described in previous publications. The remaining 70% of specimens were only taxonomically identified by experienced palaeoichthyologists, usually up to the genus level. One should remember that for ecostratigraphic purposes identifications at the genus level are very useful and, in many cases, sufficient to indicate either ecozone (for instance, identification of *Scopeloides*, *Eophycis*, *Trachinus*, *Kotlarczykia*, *Carpathichthys*) or ecological assemblage (e.g. assemblages bearing *Vinciguerria* and *Eomyctophum*, *Palaeogadus* and *Glossanodon*, *Merluccius* or *Holocentroides*). These facts, however, do not contradict the necessity of future, detailed studies pertaining to all specimens. Taking into account differentiated degree of elaboration of individual specimens, the latter have been subdivided into different categories and assigned to one of the four distinguished groups (1–4), labelled by appropriate symbols:

1. specimens described according to the obligatory rules of zoological nomenclature [group: A, C, Ł, Os];

2. specimens referred to in publications in the form of either quotation or illustration [group: B, H, PB];

3. specimens described in part or undescribed [group: R, N];

4. specimens under elaboration and revision [group: D, N].

All the described and elaborated specimens have undergone standard taxonomic verification basing on diagnostic features, descriptions, and diagnoses. The identified, although elaborated only in part, specimens (incomplete description, lack of description) have been verified on the basis of descriptions comprised in monographs and palaeontological papers by the authors of other collections. Pieces of information given in specimen labels (number of specimen, locality, exposure, level, layer, comments) have been compared with comments comprised in inventory notes and field notebooks. In case of doubtful determination, the taxon has been transferred to a higher-ranking systematic unit, and specimens unidentified to the level of taxon have been included into the group of Teleostei: Genus indet.

The catalogued material includes: complete and incomplete fish skeletons, imprints, and isolated bones and teeth, the state of preservation of which is shown in Table 3.

Apart from adult specimens, comprising the principal part of the collection, young adult (252), juveniles (444), and forms at larval stage (2) have been found as well.

The systematic catalogue of the collection Coll Fish-Carpath ZPalWr has been prepared by E. Świdnicka, basing on Nelson's (1994) classification. Minor modifications and taxon transfers to the level of another systematic unit have been made following Patterson (1993), Weitzman (1997), and Eschmeyer (1998), as well as an updated on-line version of the last paper (Froese & Pauly, 2003). Systematic terminology has been adapted from Mayr (1969).

The list of taxa has been compiled according to the following scheme:

1. taxon rank: order, suborder, family, subfamily, species, genus, *unidentified taxon;

2. material: the number of specimens falling into individual groups (given in brackets),

3. comments related to the taxa; information about the change of taxonomic name given in justified cases;

4. comments – characteristic features of the taxa given after order's description (the number of specimens in brackets); description of suborders presented for Perciformes.

The names of taxa listed below have been proposed by A. Jerzmańska and her collaborators.

Taxonomic review

Grade CHONDRICHTHIOMORPHI
Class Chondrichthyes Goodrich, 1909
Subclass Elasmobranchii Bonaparte, 1832
Superorder Euselachii Hay, 1902
*Ordo et familia indet.

Material: 4 teeth, determined as Elasmobranchii.

Order LAMNIFORMES Berg, 1940
Family ALOPIIDAE Bonaparte, 1938
Genus *Alopecias* Rafinesque, 1810

Alopecias sp.

Material: 1 tooth; described as *Alopecias* sp. (Jerzmańska & Jucha, 1963; p. 166).

Family CETORHINIDAE Gill, 1862
Genus *Cetorhinus* Blainville, 1816

Cetorhinus sp.

Material: 65 isolated filtrative processes; determined as genus *Cetorhinus*; specimens mentioned by Jerzmańska and Kotlarczyk (1988, p. 104–105).

*Familia et genus indet.

Material: 1 isolated tooth; determined as order Lamniformes.

Order HEXANCHIFORMES Berg, 1940
Family HEXANCHIDAE Gray, 1851
Genus *Hexanchus* Rafinesque, 1810

Notidanus sp.

Material: 1 isolated tooth; determined as genus *Notidanus*; change of name: *Hexanchus*.

Comments – Chondrichthyes: 3 families: Alopiidae (1), Cetorhinidae (65), Hexanchidae (1); 3 genera, 2 unidentified forms. Number of specimens in the collection: 70.

Grade TELEOSTOMI
Class Actinopterygii (Cope, 1880)
Division TELEOSTEI Müller, 1846
Order ANGUILLIFORMES Regan, 1909
Family DERICHTHYIDAE Gill, 1884 (incl. Nessoramphidae Schmidt, 1931)
Genus *Nessorhamphus* Schmidt, 1931

Nessorhamphus sp.

Material: 4 specimens; determined as genus *Nessorhamphus*; undescribed.

*Genus et species indet.

Material: 2 specimens; determined as family Nessoramphidae; specimens mentioned in the lists of taxa.

*Familia et genus indet.

Material: 33 specimens; determined as order Anguilliformes.
Comments – Anguilliformes: 1 family: Derichthyidae (6), Familia indet. (33); 1 genus, 2 unidentified forms. Number of specimens in the collection: 39.

Order CLUPEIFORMES Bleeker, 1859
Family CLUPEIDAE Bonaparte, 1831
Genus *Clupea* Linnaeus, 1758

Clupea sardinites Heckel, 1850

Material: 537 specimens, including: described (399) (Jerzmańska, 1960; p. 371; 1968, p. 390; Jerzmańska & Jucha, 1963; p. 166; Szymczyk, 1978; p. 394); undescribed (138). Species *Clupea sardinites* Heckel, 1850 has been acknowledged as a synonym of *Sardinella sardinites* (Heckel, 1850) (Daniltshenko, 1980a; p. 9; Bannikov & Parin, 1997; p. 154).

Clupea sp.

Material: 1,610 specimens, including: described in part (140) (Jerzmańska & Kotlarczyk, 1975; p. 880; Jerzmańska *et al.*, 2001), undescribed (1,470). Some specimens display properties of genus *Clupea* (Jerzmańska, 1960, 1968; Jerzmańska & Jucha, 1963; Szymczyk, 1978).

Genus *Alosa* Linck, 1790

Alosa cf. *sagorensis* Steindachner, 1863

Material: 7 specimens, described. A revision of fossil representatives of Clupeidae from the Polish Carpathians, performed on lepidological material (Szymczyk, 1978; p. 397, 401), indicated the presence of two species belonging to *Alosa*.

Alosa sp.

Material: 66 specimens, including: described (9) (Szymczyk, 1978), undescribed (57); showing properties of genus *Alosa*.

Genus *Pomolobus* Rafinesque, 1820

Pomolobus sp.

Material: 3 specimens, including: described (2) (Jerzmańska, 1968; p. 393), undescribed (1); showing properties of genus *Pomolobus*.

*Genus et species indet.

Material: 98 specimens; classified with the joint group Clupeidae; some forms display properties of genera: *Clupea* and *Alosa* (Jerzmańska, 1960, 1968; Szymczyk, 1978).

*Familia et genus indet.

Material: 1 specimen classified as the order Clupeiformes.
Comments – Clupeiformes: 1 family: Clupeidae (2321); Familia et genus indet. (1); 2 species, 3 genera, 2 unidentified forms. Number of specimens in the collection: 2,322.

Order CYPRINIFORMES Bleeker, 1859
Family CYPRINIDAE Cuvier, 1817
Genus *Barbus* Cuvier, 1817

Barbus sp.

Material: 1 scale; identified as genus *Barbus*.
Comments – Cypriniformes: 1 family: Cyprinidae; 1 form named *Barbus*.

Order OSMERIFORMES (*sensu* Nolf et Dockery, 1990)

Family ARGENTINIDAE Bonaparte, 1846

Genus *Glossanodon* Guichenot, 1867

Glossanodon musceli (Paučá, 1929)

Material: 329 specimens, including: described (294) (Jerzmańska, 1967a; p. 200; Jerzmańska, 1968; p. 394), undescribed (35); showing properties of species *G. musceli* (Paučá, 1929a)

Glossanodon sp.

Material: 148 specimens, including: described (24) (Jerzmańska, 1967a; p. 200), undescribed (124); showing properties of genus *Glossanodon* and species *G. musceli*.

*Genus et species indet.

Material: 14 specimens, classified with the joint group Argentinidae; some specimens display properties of genus *Glossanodon*.

Family BATHYLAGIDAE Gill, 1884

Genus *Idrissia* Arambourg, 1954

Idrissia carpathica Jerzmańska, 1960

Material: 51 specimens. Holotype: ZPALWr Os/164; Sobniów [SO].

1960. *Idrissia carpathica* nov. sp.; A. Jerzmańska, p. 372, pl. I, Fig. 1.

Including: specimens described (46) (Jerzmańska, 1960; p. 371), undescribed (5). Contribution about transferring *Idrissia carpathica* to the family Bathylagidae (Jerzmańska & Kotlarczyk, 1981; p. 70). There are no data that would justify, following Weitzman's (1974) suggestion, classification of *I. carpathica* to the family Photichthyidae.

Idrissia sp.

Material: 211 specimens, classified with the joint group *Idrissia*. Including: specimens mentioned (31) (Jerzmańska, 1960; p. 371), undescribed (180); showing properties of the genus *Idrissia*.

*Genus et species indet. (Melania)

Material: 34 specimens; classified as a new form; informal name (Melania) proposed by A. Jerzmańska in the years 1989–1991 for the form Bathylagidae. In the index of taxa (Kotlarczyk, 1985; p. 56–57), the form called Melania was erroneously classified among Chondrichthyes.

*Genus et species indet.

Material: 26 specimens; classified with the joint group Bathylagidae.

Family ALEPOCEPHALIDAE Richardson, 1856

Genus *Carpathichthys* Jerzmańska, 1979

Carpathichthys polonicus Jerzmańska, 1979

Material: 27 specimens, described. Holotype: ZPALWr A/2004; Krępak [KIII].

1979. *Carpathichthys polonicus* nov. sp.; A. Jerzmańska, p. 65, pls. 15, 16, text figs. 1, 5B, 6.

Carpathichthys sp.

Material: 15 specimens; identified to the level of genus *Carpathichthys*; showing properties of species *C. polonicus* (Jerzmańska, 1979; p. 65).

Genus *Bathypriion* Marshall, 1966

Bathypriion sp.

Material: 1 specimen; identified to the level of genus *Bathypriion*; undescribed.

*Genus et species indet.

Material: 9 specimens; classified with the joint group Alepocephalidae.

Comments – Osmeriformes: 2 holotypes; 3 families: Argentinidae (491), Bathylagidae (322), Alepocephalidae (52); 3 species, 4 genera, 4 unidentified forms. Synonymy given in papers by: Jerzmańska (1960, p. 7; 1967a, p. 200; 1979, p. 66). Number of specimens in the collection: 865.

Order SALMONIFORMES (*sensu* Berg, 1940)

*Familia et genus indet.

Material: 2 specimens; identified to the level of order Salmoniformes.

Familia Incertae sedis

*Genus et species indet. (xx)

Material: 20 specimens; classified as a new form Salmoniformes? (xx); informal name proposed by A. Jerzmańska in the years 1989–1993.

Comments – Salmoniformes: 2 families: Familia Incertae sedis (20), Familia indet. (2); 2 unidentified forms. Number of specimens in the collection: 22.

Order STOMIIFORMES (*sensu* Harold et Weitzman, 1996)

Family GONOSTOMATIDAE Gill, 1893

Genus *Scopeloides* Wettstein, 1886

Scopeloides glarisianus (Agassiz, 1844)

Material: 39 specimens, including: described (33) (Jerzmańska, 1968; p. 395), undescribed (6); showing properties of species *S. glarisianus*.

Scopeloides sp.

Material: 178 specimens; classified with the joint group *Scopeloides*; including: described (1) (Jerzmańska, 1968; p. 395), undescribed (177).

Genus *Kotlarczykia* Jerzmańska, 1974

Kotlarczykia bathybia Jerzmańska, 1974

Material: 29 specimens. Typical species (holotype): ZPALWr A/1998; Krępak [KIV₄].

1974. *Kotlarczykia bathybia* nov. sp.; A. Jerzmańska, p. 285, pl. XXIII, dimensions: p. 258.

Including: specimens described (5) (Jerzmańska, 1974; p. 284); described in part (24) (Kotlarczyk & Jerzmańska, 1976).

Kotlarczykia sp.

Material: 11 specimens; identified to the level of genus *Kotlarczykia*; showing properties of species *K. bathybia* (Jerzmańska, 1974; p. 285).

*Genus et species indet.

Material: 84 specimens; classified with the joint group Gonostomatidae.

Family STERNOPTYCHIDAE Duméril, 1806

Genus *Polyipnus* Günther, 1887

Polyipnus brevis Horbatsh, 1961

Material: 77 specimens; identified to the level of species *P. brevis*;

including: mentioned specimens (77) (Jerzmańska & Kotlarczyk, 1979; p. 47; 1981, p. 71). Description and diagnosis (Horbatsch, 1961b; p. 168). Archival data bear descriptions made by A. Jerzmańska, and a note suggesting to change the generic name *Polyipnus* for a species derived from the Polish Carpathians: *Horbatschia brevis* (Horbatsch, 1961). Change of name introduced by Prokofiev (2002a, p. 28).

Polyipnus anteaeroides Ciobanu, 1977

Material: 14 specimens; identified to the rank of species *P. cf. anteaeroides* by A. Jerzmańska.

Polyipnus sobniowiensis Jerzmańska, 1960

Material: 128 specimens. Holotype: ZPALWr Os/49; Sobniów [SO]. 1960. *Polyipnus sobniowiensis* nov. sp.; A. Jerzmańska, p. 379, 380, pl. II, Fig. 1. Including: specimens described (111) (Jerzmańska, 1960; p. 379; Jerzmańska & Jucha, 1963; p. 166–167), undescribed (17). *P. sobniowiensis* from the Polish Carpathians (Jerzmańska, 1960) and *P. oligocenicus* from the Romanian Carpathians (Ciobanu, 1977) belong, according to Prokofiev, to an hitherto-undescribed genus (Prokofiev, 2002a; p. 30).

Polyipnus cf. sobniowiensis Jerzmańska, 1960

Material: 16 specimens; mentioned.

Polyipnus sp.

Material: 104 specimens; classified with the joint group *Polyipnus*. Some of the forms display species' properties (Jerzmańska, 1960; Jerzmańska & Jucha, 1963; Ciobanu, 1977; Prokofiev, 2002a).

Genus *Argyropelecus* Cocco, 1829

Argyropelecus cosmovicii Cosmovici et Paucă, 1943

Material: 24 specimens, including: described (21) (Jerzmańska, 1968; p. 401), undescribed (3); showing properties of species *A. cosmovicii*.

Argyropelecus sp.

Material: 304 specimens; classified with the joint group *Argyropelecus*. Some of the forms display properties of species *A. cosmovicii* (Jerzmańska, 1968; p. 401).

*Genus et species indet. (xz)

Material: 151 specimens; classified as a new form; informal name Sternoptychidae (xz) proposed by A. Jerzmańska in the years 1986–1990. Archival records bear partial descriptions and hand-made drawings of this group of specimens.

*Genus et species indet.

Material: 59 specimens; classified with the joint group Sternoptychidae.

Family PHOTICHTHYIDAE Weitzman, 1974

Genus *Vinciguerria* Jordan et Evermann, 1896

Vinciguerria talgiensis Daniltshenko, 1946

Material: 3 specimens; identified to the level of species *V. talgiensis*; showing properties compatible with those described by Daniltshenko (1946; p. 641; 1980a, p. 38).

Vinciguerria obscura Daniltshenko, 1946

Material: 44 specimens; including: described (36) (Jerzmańska,

1968; p. 398); diagnosis (Daniltshenko, 1946, p. 641; 1960, p. 21; 1980a, p. 39), undescribed (8); showing properties compatible with species' description.

Vinciguerria distincta Daniltshenko, 1962

Material: 36 specimens; including: described (19) (Jerzmańska, 1968; p. 399); diagnosis (Daniltshenko 1962, p. 112), undescribed (17); showing properties compatible with species' description. R. Gregorová, described the above three species as *V. obscura* (Gregorová, 2000; p. 160).

Vinciguerria merklini Daniltshenko, 1946

Material: 2 specimens; identified to the level of species; showing species' properties (Daniltshenko, 1946, p. 641; 1980a, p. 40).

Vinciguerria sp.

Material: 179 specimens; classified with the joint group *Vinciguerria*; including: specimens described as *Vinciguerria* sp. (61) (Jerzmańska, 1968; p. 399); undescribed (118) identified to the level of genus *Vinciguerria*. Basing on a revision of fossil forms *Vinciguerria* Jordan et Everman, 1896 from the Moravian Carpathians, the Oligocene species of genus *Vinciguerria* Goode et Bean, 1895 from the Polish Carpathians (Jerzmańska, 1960, 1968) have been transferred from family Gonostomatidae to family Phothichthyidae (Gregorová, 1989; p. 87–100).

*Familia et genus indet.

Material: 13 specimens; identified to the order Stomiiformes. Comments – Stomiiformes: 2 holotypes; 3 families: Gonostomatidae (341), Sternoptychidae (877), Phothichthyidae (264), Familia indet. (13); 10 species; 5 genera, 5 unidentified forms. Number of specimens in the collection: 1,495.

Order AULOPIFORMES Rosen, 1973

Family PARALEPIDIDAE Gill, 1872

Genus *Holosteus* Agassiz, 1839

Holosteus mariae (Menner, 1948)

Material: 1 specimen; identified to the level of species *H. mariae*; description (Menner, 1948; p. 52). This taxon has been quoted from Rudawka Rymanowska site by Bieńkowska (2004, p. 188–189).

Holosteus sp.

Material: 51 specimens; identified to the level of genus *Holosteus*; archival records include incomplete descriptions of specimens made by A. Jerzmańska.

*Genus et species indet.

Material: 6 specimens; classified with the family Paralepididae. Comments – Aulopiformes: 1 family: Paralepididae; 1 species, 1 genus, 1 unidentified form. Number of specimens in the collection: 58.

Order MYCTOPHIFORMES Regan, 1911

Family MYCTOPHIDAE Gill, 1893

Subfamily MYCTOPHINAE Gill, 1893

Genus *Eomyctophum* Daniltshenko, 1947

Eomyctophum limicola Daniltshenko, 1960

Material: 105 specimens; including: described (39) (Jerzmańska, 1968; p. 406), undescribed (66); showing properties of the species *E. limicola*.

Eomyctophum cf. koraense Daniltshenko, 1947

Material: 124 specimens; including: described (109) (Jerzmańska,

1960, p. 398; 1968, p. 409; Jerzmańska & Jucha, 1963), undescribed (15).

Eomyctophum menneri Daniltschenko, 1947

Material: 85 specimens; including: described (17) (Jerzmańska, 1960, p. 396; 1968, p. 408); undescribed (68); showing properties of the species *E. menneri* (Daniltschenko, 1947b)

Eomyctophum sp.

Material: 1,331 specimens; classified with the joint group *Eomyctophum*. Including: specimens described as *Eomyctophum* sp. (207) (Jerzmańska, 1960; Jerzmańska & Jucha, 1963; Jerzmańska & Kotlarczyk, 1975); undescribed (1,124); identified as *Eomyctophum*; some specimens display properties of the above-mentioned species.

Genus *Protomyctophum* Fraser-Brunner, 1949

Protomyctophum sp.

Material: 4 specimens; identified to the level of genus *Protomyctophum*.

Subfamily LAMPANYCTINAE Gill, 1893

Genus *Diaphus* Eigenmann et Eigenmann, 1890

Diaphus sp.

Material: 1 specimen; identified to the level of genus *Diaphus*. Gregorová (2000) acknowledged one species described from Moravia as *Diaphus moravicus* Kalabis, 1948 as a synonym of *Oligophus moravicus*.

*Genus et species indet. (Giant II)

Material: 16 specimens; classified as a new form; informal name Myctophidae (Giant II) proposed by A. Jerzmańska in the years 1989–1990.

*Genus et species indet.

Material: 16 specimens; classified with the joint group Myctophidae.

*Familia et genus indet.

Material: 1 specimen; included into the order Myctophiformes (?). Comments – Myctophiformes: 1 family: Myctophidae (1682), Familia indet. (1); 3 species, 3 genera, 3 unidentified forms. Number of specimens in the collection: 1683.

Order GADIFORMES Goodrich, 1909 (Cohen, 1989)

Family MORIDAE Goode et Bean, 1896

*Genus et species indet.

Material: 1 specimen; identified to the level of family Moridae.

Family BREGMACEROTIDAE Gill, 1872

Genus *Bregmaceros* Thompson, 1840

Bregmaceros filamentosus (Priem, 1908)

Material: 29 specimens; identified and described as *B. filamentosus* (Świdnicki, 1990; p. 14).

Bregmaceros sp.

Material: 8 specimens; including: described (7); undescribed (1); showing properties of the species *B. filamentosus*.

Family PHYCIDAE Swainson, 1838

Genus *Eophycis* Jerzmańska, 1968

Eophycis jamnensis Jerzmańska, 1968

Material: 15 specimens, described (Jerzmańska, 1968; Świdnicki,

1990); diagnosis and description (Jerzmańska, 1968; p. 413). Holotype: ZPALWr A/839; Jamna [J].

1968. *Eophycis jamnensis* nov. gen. et sp.; A. Jerzmańska, p. 413, pl. III, Fig. 3, text-Fig. 8.

Eophycis sp.

Material: 4 specimens; undescribed; showing properties of a genus (Jerzmańska, 1968; p. 413).

Genus *Onobrosmius* Bogatshov, 1938

Onobrosmius sp.

Material: 4 specimens; identified to the level of genus *Onobrosmius*. Owing to a revision of the Caucasian representatives of Moridae, *Onobrosmius* has been transferred to the subfamily Phycinae (Świdnicki *et al.*, 1990; p. 503).

Genus *Pseudoraniceps* Fedotov, 1974

Pseudoraniceps sp.

Material: 1 specimen; undescribed; showing properties of the genus *Pseudoraniceps* (Fedotov, 1974; p. 84). Owing to a revision of Caucasian holotypes, *Pseudoraniceps* has been acknowledged as a younger synonym of *Onobrosmius* (Świdnicki *et al.*, 1990; p. 503–504).

Family MERLUCCIIDAE Adams, 1864 (*sensu* Cohen, 1973)

Subfamily MERLUCCIINAE Jordan et Gilbert, 1883

Genus *Palaeogadus* Rath, 1859

Palaeogadus abbreviatus (Bogatshov, 1933)

Material: 1 specimen; identified to the level of species; described (Jerzmańska, 1968; p. 421).

Palaeogadus simionescui (Simionescu, 1905)

Material: 238 specimens; including: described (192) (Jerzmańska, 1968; Świdnicki, 1990; p. 31–36); diagnosis and synonymy (Jerzmańska, 1968; p. 417); undescribed (46); showing properties of the species *P. simionescui*.

Palaeogadus carpathicus sp. nov. Świdnicki, 1991

Material: 2 specimens; identified in 1991 by J. Świdnicki to the level of a new species; archival records bear no description of this form.

Palaeogadus distinctus sp. nov. Świdnicki, 1990

Material: 53 specimens, described (Świdnicki, 1990; p. 23). Holotype: ZPALWr C/37; Błażowa [B4]. 1990. *Palaeogadus distinctus* sp. nov.; J. Świdnicki, p. 23–31, fot. 1, Fig. 19. [syn.1968. *Merluccius inferus* Daniltschenko, 1947a: A. Jerzmańska, p. 424, text-Fig. 11].

Palaeogadus intergerinus Daniltschenko, 1947a

Material: 15 specimens; identified to the level of species *P. intergerinus*; showing properties of a species (Daniltschenko, 1947; p. 660).

Palaeogadus sp.

Material: 100 specimens; classified with the joint group *Palaeogadus*. Including: specimens described as *Palaeogadus* sp. (2) belonging to the oldest representative of Gadiformes (Świdnicki, 1990; p. 38–41); undescribed (98); some specimens display properties of the above species (Jerzmańska, 1968; Świdnicki, 1990).

Genus *Merluccius* Rafinesque, 1810

Merluccius errans (Smirnov, 1935)

Material: 6 specimens; described (Świdnicki, 1990; p. 43–44); diagnosis for a typical species (Smirnov, 1935; p. 67).

Merluccius hartensis sp. nov. Świdnicki, 1990

Material: 4 specimens; described (Świdnicki, 1990; p. 44). Holotype: ZPALWr H/80; Harta [HT].

1990. *Merluccius hartensis* sp. nov.; J. Świdnicki, p. 44–52.

Merluccius sp.

Material: 145 specimens; classified with the joint group *Merluccius*; including: mentioned as *Merluccius* sp. (10); undescribed (135); this group of specimens includes representatives of the described species (Jerzmańska, 1968; Świdnicki, 1990).

Subfamily STEINDACHNERIINAE Marshall et Cohen, 1973

Genus *Parasteindachneria* genus nov. Świdnicki, 1990

Parasteindachneria oligoacena sp. nov. Świdnicki, 1990

Material: 6 specimens, described (Świdnicki, 1990; p. 53). Holotype: ZPALWr C/117; Przysietnica [PS_{8a}]. 1990. *Parasteindachneria oligoacena* sp. nov.; J. Świdnicki, p. 53–57.

[syn.1968. *Merluccius macroactus* (Kramberger, 1879); A. Jerzmańska, p. 422, Fig. 10]

Family GADIDAE Rafinesque, 1810

Subfamily LOTINAE Jordan et Evermann, 1898

Genus *Palaemolva* Daniltshenko, 1947

Palaemolva monstrata Fedotov, 1974

Material: 2 specimens; identified to the level of species *P. monstrata*; showing species' properties (Fedotov, 1974, p. 87; 1976, p. 48).

Palaemolva sp.

Material: 6 specimens; identified to the level of genus; showing properties of a genus *Palaemolva* (Daniltshenko, 1947a, p. 2053; 1960, p. 42).

*Genus et species indet.

Material: 54 specimens; undescribed; classified with the joint group Gadidae.

*Familia et genus indet.

Material: 100 specimens; classified with the order Gadiformes. Including: specimens described (1) (Świdnicki, 1990; p. 64–66); mentioned (11) (Jerzmańska *et al.*, 2001; p. 27); undescribed (88). Comments – Gadiformes: 5 holotypes; 5 families: Moridae (1), Bregmacerotidae (37), Phycidae (24), Merlucciidae (576), Gadidae (62), Familia et genus indet. (100); 11 species, 6 genera, 3 unidentified forms. Number of specimens in the collection: 800.

Order OPHIDIIFORMES Berg, 1937

Family OPHIDIIDAE Rafinesque, 1810

Genus *Propteridium* Arambourg, 1967

Propteridium sp.

Material: 1 specimen; identified to the genus *Propteridium*; showing properties of a genus (Arambourg, 1967; p. 130).

Genus *Glyptophidium* Alcock, 1889

Glyptophidium sp.

Material: 8 specimens; including: described (1) (Świdnicki, 1988b; p. 401–404); undescribed (7); showing properties of the ge-

nus *Glyptophidium*.

*Genus et species indet.

Material: 2 specimens; identified by A. Jerzmańska as Brotulidae.

*Familia et genus indet.

Material: 5 specimens; classified with the order Ophidiiformes. Comments – Ophidiiformes: 1 family: Ophidiidae (11), Familia indet. (5); 2 genera of the species rank, 2 unidentified forms. Number of specimens in the collection: 16.

Order LOPHIIFORMES Garman, 1899

Family ANTENNARIIDAE Gill, 1863

*Genus et species indet.

Material: 3 specimens; identified to the level of family Antennariidae.

Family CERATIIDAE (*sensu* Berg, 1940)

*Genus et species indet.

Material: 4 specimens; identified to the level of family Ceratiidae. Comments – Lophiiformes: 2 families: Antennariidae (3), Ceratiidae (4); 2 unidentified forms. Number of specimens in the collection: 7.

Order MUGILIFORMES (*sensu* Johnson et Patterson, 1993)

Family MUGILIDAE Cuvier, 1829

Genus *Mugil* Linnaeus, 1758

Mugil sp.

Material: 1 specimen; identified as *Mugil* sp.

Comments – Mugiliformes: 1 family: Mugilidae; 1 form *Mugil*. Number of specimens in the collection: 1.

Order BELONIFORMES Berg, 1937

Family HEMIRAMPHIDAE Gill, 1861

Genus *Hemiramphus* Cuvier, 1817

Hemiramphus jerzyi Jerzmańska, 1968

Material: 3 specimens; described (Jerzmańska, 1968; p. 410). Holotype: ZPALWr A/895; Rudawka Birczańska [RB₃]. 1968. *Hemiramphus georgii* nov. sp.; A. Jerzmańska, p. 410, pl. II, Fig. 1, text-Fig. 7A, C, dimensions: p. 410.; 1985. *Hemiramphus jerzyi* nom. nov.; A. Jerzmańska, p. 110.

Comments – Beloniformes: 1 holotype; 1 family: Hemiramphidae; 1 species. Number of specimens in the collection: 3.

Order BERYCIFORMES Regan, 1909

Family TRACHICHTHYIDAE Bleeker, 1859

Genus *Africentrum* (*sensu* White E. I. et Moy-Thomas J. A., 1941)

Africentrum sp.

Material: 173 specimens; classified with the joint group *Africentrum*. Authors are not sure whether all specimens identified by A. Jerzmańska as *Africentrum* sp. can be transferred to the genus *Holocentroides* without detailed osteological analysis. In this paper, we use both the names: *Africentrum* (Trachichthyidae) and *Holocentroides* (Holocentridae). The generic name *Africentrum* was introduced into zoological nomenclature by White and Moy-Thomas (1941).

*Genus et species indet.

Material: 1 specimen; identified to the level of family Trachichthyidae.

Family BERYCIDAE Gill, 1862

Genus *Paraberyx* gen. nov. Jerzmańska, 1975*Paraberyx bachoviensis* sp. nov. Jerzmańska, 1975

Material: 3 specimens, classified as a new species; unpublished. Holotype: ZPALWr A/2002; Bachów [BH₁]. 1975. Berycidae.; Jerzmańska & Kotlarczyk, p. 881. The generic and species name *Paraberyx bachoviensis* was proposed by A. Jerzmańska in 1975 (hand-written notes concerning description of the genus and species). Information about a new form (Berycidae: Genus indet.) present at site Bachów was published by Jerzmańska and Kotlarczyk (1975; p. 880). In 1989, A.F. Bannikov suggested that this form is a representative of the family Holocentridae (note from archival label).

Paraberyx sp.Material: 4 specimens; identified to the level of genus *Paraberyx*.

*Genus et species indet.

Material: 1 specimen; identified to the level of family Berycidae.

Family HOLOCENTRIDAE Richardson, 1846

Genus *Holocentroides* Paucă, 1931*Holocentroides moldavicus* Paucă, 1931 (= *Africentrum moldavicum* (Paucă 1931))

Material: 56 specimens; identified as *A. moldavicum*; including: mentioned (49); incomplete descriptions made by A. Jerzmańska; undescribed (7). *A. moldavicum* (Paucă, 1931) has been mentioned in some biostratigraphical works (Jerzmańska & Kotlarczyk, 1975, p. 880; 1981, p. 64; Kotlarczyk, 1985, p. 56–57), whereas *H. moldavicus* Paucă, 1931 has been quoted by Kotlarczyk and Jerzmańska (1980, p. 108; 1988a, p. 349) and Jerzmańska and Kotlarczyk (1988, p. 104–105). The form *Holocentroides moldavicus* Paucă 1931 found at Beograd site was shifted by Andelkovitsh (1969, 1989) from family Berycidae (cf. Paucă, 1931) to family Holocentridae.

Holocentroides sp.Material: 173 specimens; identified to the level of genus *Holocentroides*.

*Familia et genus indet.

Material: 55 specimens; classified with the order Beryciformes. Comments – Beryciformes: 1 holotype; 3 families: Trachichthyidae (174), Berycidae (8), Holocentridae (229), Familia indet. (55); 2 species, 3 genera, 3 unidentified forms. Number of specimens in the collection: 466.

Order ZEIFORMES Regan, 1909 (*sensu* Greenwood *et al.*, 1966)

Family ZEIDAE Bonaparte, 1831

Genus *Zenopsis* Gill, 1862*Zenopsis clarus* Daniltshenko, 1960

Material: 3 specimens; including: described (2) (Świdnicki, 1986; p. 119); undescribed (1).

Zenopsis sp.

Material: 8 specimens; including: described (1) (Jerzmańska, 1968, p. 441; Świdnicki, 1986); undescribed (7).

Genus *Zeus* Linnaeus, 1758*Zeus faber* Linnaeus, 1758

Material: 11 specimens; including: described (9) (Świdnicki, 1986; p. 114); undescribed (2).

Zeus sp.Material: 27 specimens; identified to the level of genus *Zeus*; showing properties of a genus.

*Genus et species indet.

Material: 4 specimens; identified to the level of family Zeidae.

*Familia et genus indet.

Material: 5 specimens; classified with the order Zeiformes.

Comments – Zeiformes: 1 family: Zeidae (53), Familia indet. (5); 2 species, 2 genera, 2 unidentified forms. Number of specimens in the collection: 58.

Order CAPROIFORMES (*sensu* Santini et Tyler, 2003)

Family CAPROIDAE Lowe, 1844

Genus *Antigonia* Lowe, 1843*Antigonia* sp.

Material: 53 specimens; including: described (14) (Świdnicki, 1986, p. 130; 1988, p. 251); undescribed (39); showing properties of a genus.

Genus *Capros* Lacépède, 1802*Capros radobojanus* (Kramberger, 1882)

Material: 45 specimens; including: described (44) (Jerzmańska, 1968, p. 443; Świdnicki, 1986, p. 123); undescribed (1).

Capros medianus Świdnicki, 1986Material: 4 specimens; identified to the level of species; including: specimens described (3) (Świdnicki, 1986; p. 124); undescribed (1). Holotype: ZPALWr A/2059; Błażowa [Ba]. 1986. *Capros medianus* nov. sp.; J. Świdnicki, p. 124, 125, pl. 47, text figs.: 6C, 7, 8B, C, 10B.*Capros* sp.Material: 10 specimens; identified to the level of genus *Capros*; undescribed.

*Genus et species indet.

Material: 3 specimens; identified to the level of family Caproidae. Comments – Caproiformes: 1 holotype; 1 family: Caproidae; 2 species, 1 genus of the species rank, 1 unidentified form. Species transferred to the order Caproiformes (Santini & Tyler, 2003, p. 610; Tyler *et al.*, 2003). Number of specimens in the collection: 115.

Order GASTEROSTEIFORMES Goodrich, 1909

Family AULORHYNCHIDAE Gill, 1861

*Genus et species indet.

Material: 4 specimens; identified to the level of family Aulorhynchidae.

Family SOLENOSTOMIDAE Kaup, 1853

Genus *Solenorhynchus* Heckel, 1854*Solenorhynchus* sp.Material: 1 specimen; identified as *Solenorhynchus*; form considered extinct in the Eocene (Berg, 1955).

Family SYNGNATHIDAE Rafinesque, 1810

Subfamily SYNGNATHINAE Duncker, 1912

Genus *Syngnathus* Linnaeus, 1758*Syngnathus incompletus* Cosmovici, 1887

Material: 50 specimens; including: described (17 specimens);

diagnosis and description Cosmovici, 1887, p. 99; Jerzmańska, 1968, p. 440); undescribed (33); nearly 50% of the material shows species' properties.

Syngnathus sp. A

Material: 46 specimens; classified as a new form; informal name *Syngnathus* sp. (A) proposed by A. Jerzmańska in order to distinguish a new species.

Syngnathus sp. B

Material: 2 specimens; classified as a new form; informal name *Syngnathus* sp. (B) proposed by A. Jerzmańska in order to distinguish a new species.

Syngnathus sp.

Material: 627 specimens; classified with the joint group *Syngnathus*. Including: specimens described as *Syngnathus* sp. (6) (Jerzmańska, 1968; p. 440); mentioned (143) (Jerzmańska & Kolarczyk, 1975, p. 883, 885; Jerzmańska *et al.*, 2001); undescribed (478); showing properties of the genus *Syngnathus*.

Subfamily EOGASTROPHINAE Jerzmańska, 1968

Genus *Hipposyngnathus* Daniltshenko, 1960

Hipposyngnathus neriticus Jerzmańska, 1968

Material: 50 specimens; described (50) (Jerzmańska, 1968; p. 437). Holotype: ZPALWr A/533; Jamna Dolna [J]. 1968. *Hipposyngnathus neriticus* nov. sp.; A. Jerzmańska, p. 437, pl. VII, Fig. 2, text-Fig. 16D.

*Genus et species indet.

Material: 3 specimens; identified to the level of family Syngnathidae.

Family AULOSTOMIDAE Latreille, 1825

*Genus et species indet.

Material: 3 specimens; identified to the level of family Aulostomidae; undescribed.

Family FISTULARIIDAE Bonaparte, 1832

Genus *Fistularia* Linnaeus, 1758

Fistularia sp.

Material: 12 specimens; identified to the level of genus *Fistularia*; undescribed; showing properties of a genus (Daniltshenko, 1960; p. 74).

*Genus et species indet.

Material: 1 specimen; identified to the level of family Fistularidae.

Family CENTRISCIDAE Rafinesque, 1826 (*sensu* Berg, 1955)

Genus *Centriscus* Linnaeus, 1758

Centriscus heinrichi (Heckel, 1850)

Material: 14 specimens; including: described (11), determined gender: females (4); males (7) (Jerzmańska, 1968; p. 432); undescribed (3); showing species' properties.

Centriscus longispinus Rozhdestvenski, 1949

Material: 11 specimens; including: described (9) (Jerzmańska, 1968; p. 427); undescribed (2); showing species' properties (Rozhdestvenski 1949, p. 1167).

Centriscus teleajensis (Jonet, 1949)

Material: 9 specimens; including: described (8) (Jerzmańska,

1968; p. 431); diagnosis (Jonet, 1949; p. 360); undescribed (1); showing species' properties.

Centriscus sp. nov. (x)

Material: 28 specimens; classified as a new form; informal name *Centriscus* sp. (x) proposed by A. Jerzmańska in the years 1984–1987 (archival manuscript of A. Jerzmańska, bearing descriptions and drawings).

Centriscus sp.

Material: 533 specimens; classified with the joint group *Centriscus*; including: described (31) (Jerzmańska, 1968; p. 433); undescribed (502); showing properties of the genus *Centriscus*. Nearly 25 % of specimens probably belong to a new form *Centriscus* (x).

*Familia et species indet.

Material: 9 specimens; classified with the order Syngnathiformes. Comments – Gasterosteiformes: 1 holotype; 6 families: Aulorhynchidae (4), Solenostomidae (1), Syngnathidae (778), Aulostomidae (3), Fistulariidae (13), Centriscidae (595), Familia indet. (9); 5 species, 3 genera of the species rank, 4 genera, 4 unidentified forms. Number of specimens in the collection: 1,403.

Order SCORPAENIFORMES Garman, 1899

Suborder SCORPAENOIDEI Garman, 1899

Family SCORPAENIDAE Risso, 1826

Genus *Scorpaenoides* Priem, 1899

Scorpaenoides popovicii Priem, 1899

Material: 1 specimen; identified to the level of species.

Scorpaenoides sp.

Material: 60 specimens; identified to the level of genus *Scorpaenoides*; undescribed.

Genus *Scorpaena* Linnaeus, 1758

Scorpaena sp.

Material: 1 specimen; identified to the level of genus *Scorpaena*.

*Genus et species indet.

Material: 1 specimen; identified to the level of family Scorpaenidae.

Suborder COTTOIDEI Bleeker, 1859

Family COTTIDAE Swainson, 1839

*Genus et species indet.

Comment: 7 specimens; identified to the level of family Cottidae (Jerzmańska, 1960; p. 404, pl. IV, Fig. 2), as a result of a revision, transferred by A. Jerzmańska to the family Gempylidae (*Thyrsitoides* sp., *Hemithyrsites* sp.)

*Familia et genus indet.

Material: 1 specimen; classified with the order Scorpaeniformes. Comments – Scorpeniformes: 1 family: Scorpaenidae (63), Familia indet. (1); 1 species, 2 genera, 2 unidentified forms. Number of specimens in the collection: 64.

Order PERCIFORMES Bleeker, 1859

Suborder PERCOIDEI Bleeker, 1859

Family SERRANIDAE Richardson, 1846

Genus *Properca* Sauvage, 1880

Properca sabbai Paucă, 1929

Material: 11 specimens; including: described (7) (Jerzmańska,

1968; p. 446); diagnosis (Paučá, 1929a; p. 117); undescribed (4); showing properties of the species *P. sabbai*.

Properca sp.

Material: 7 specimens; undescribed; showing properties of the genus *Properca*.

Genus *Serranus* Cuvier, 1817

Serranus budensis (Heckel, 1856)

Material: 439 specimens; including: described (345) (Jerzmańska, 1968; p. 449); diagnosis (Weiler, 1933, p. 12–13; Daniltshenko, 1960, p. 101); mentioned or undescribed (94); showing properties of the species *S. budensis*.

Serranus sp.

Material: 302 specimens; identified to the level of genus *Serranus*; showing properties of a genus (Weiler, 1933; Daniltshenko, 1960; Jerzmańska, 1968).

*Genus et species indet.

Material: 6 specimens; identified as Serranidae (?).

Family PERCIDAE Cuvier, 1817

Genus *Propercarina* Paučá, 1929

Propercarina sp.

Material: 7 specimens; identified as *Propercarina*; showing properties of a genus (Paučá, 1929b).

Family PRIACANTHIDAE Gill, 1872

Genus *Priacanthus* Oken, 1817

Priacanthus longispinus Lednev, 1914

Material: 4 specimens; identified to the level of species (Jerzmańska & Jucha, 1963; p. 170); diagnosis (Lednev, 1914, p. 16; Daniltshenko, 1960, p. 107).

Priacanthus sp.

Material: 8 specimens; identified to the level of genus *Priacanthus*; specimens earlier identified as *Apostasis* sp. have been transferred by A. Jerzmańska to the genus *Priacanthus*.

Family APOGONIDAE Jordan et Gilbert, 1882

*Genus et species indet.

Material: 42 specimens; identified to the level of family Apogoniidae.

Family ECHENEIDAE Rafinesque, 1810

Genus *Echeneis* Linnaeus, 1758

Echeneis carpathica Szajnocha, 1926

Material: 20 specimens; cited (Jerzmańska & Kotlarczyk, 1981, p. 64), incl. 8 specimens described (Jerzmańska & Świdnicka, 2003, p. 254).

*Genus et species indet.

Material: 1 specimen; identified to the level of family Echeneidae.

Family CARANGIDAE Rafinesque, 1815

Genus *Caranx* Lacépède, 1802

Caranx petrodavae Simionescu, 1905

Material: 5 specimens; identified to the level of species; no description.

Caranx gracilis Kramberger, 1882

Material: 3 specimens; identified to the level of species; mentioned (Jerzmańska et al., 2001).

Caranx sp.

Material: 3 specimens; identified as *Caranx* sp.; showing properties of a genus (Lacépède, 1802, p. 57; Günther, 1860, p. 422).

Genus *Archaeus* Agassiz, 1844

Archaeus sp.

Material: 2 specimens; identified to the level of genus *Archaeus*; mentioned (Jerzmańska & Kotlarczyk, 1975; p. 880); genus description (Agassiz, 1833–1834, p. 49; Daniltshenko, 1960, p. 112).

*Genus et species indet.

Material: 7 specimens; identified to the level of family Carangidae (5); Carangidae (?) (2).

Family LEIOGNATHIDAE Jordan, 1923

Genus *Leiognathus* Lacépède, 1803

Leiognathus cf. *minutus* Daniltshenko, 1980

Material: 22 specimens; described (Jerzmańska et al., 2001); species description (Daniltshenko, 1980a; p. 133).

Leiognathus sp.

Material: 3 specimens; identified to the level of genus *Leiognathus*.

Genus *Equula* Cuvier, 1815

Equula ? sp.

Material: 1 specimen; described (Jerzmańska, 1960; p. 401). Genus *Equula* is indicated in the family Leiognathidae (Eschmayer, 1998).

Family CHAETODONTIDAE Bonaparte, 1832

Genus *Forcipiger* Jordan et McGregor, 1898

Forcipiger sp.

Material: 2 specimens; identified to the level of genus; undescribed.

*Familia et genus indet.

Material: 9 specimens; identified to the level of suborder Percoidei.

Comments – Percoidei: 8 families: Serranidae (765), Percidae (7), Priacanthidae (12), Apogonidae (42), Echeneidae (21), Carangidae (20), Leiognathidae (26), Chaetodontidae (2), Familia indet. (9); 7 species, 9 genera, 5 unidentified forms. Number of specimens in the collection: 904.

Suborder TRACHINOIDEI Bertin et Arambourg, 1958

Family AMMODYTIDAE Bonaparte, 1846

Genus *Ammodytes* Linnaeus, 1758

Ammodytes antipai Paučá, 1929

Material: 37 specimens; including: described (19) (Jerzmańska, 1968; p. 467); diagnosis (Paučá, 1929a; p. 115); undescribed (18); showing properties of the species *A. antipai*.

Ammodytes sp.

Material: 18 specimens; identified to the level of genus *Ammodytes*; undescribed.

Family TRACHINIDAE Risso, 1826

Genus *Trachinus* Linnaeus, 1758

Trachinus minutus (Jonet, 1958)

Material: 158 specimens; described (Jerzmańska, 1968; p. 453); diagnosis (Jonet, 1958; p. 55).

Trachinus sp.

Material: 12 specimens; identified to the level of genus *Trachinus*; showing properties of a genus (Jerzmańska, 1968; p. 453).

Comments – Trachinoidei: 2 families: Ammodytidae (37); Trachinidae (170); 2 species, 2 genera. Number of specimens in the collection: 207.

Suborder GOBIOIDEI Jordan et Evermann, 1896

Family GOBIIDAE Bonaparte, 1831

Genus *Gobius* Linnaeus, 1758

Gobius sp.

Material: 1 specimen; identified to the level of genus *Gobius* (Jerzmańska *et al.*, 2001); description (Arambourg, 1927; p. 193).

Comments – Gobioidae: 1 family: Gobiidae; 1 genus *Gobius*.

Suborder ACANTHUROIDEI *s.s.* (Tyler *et al.*, 1989)

Family ACANTHURIDAE Bleeker, 1859

Genus *Caprovesposus* Daniltshenko, 1960

Caprovesposus sp.

Material: 1 specimen; identified to the level of genus *Caprovesposus*; description (Daniltshenko, 1960; p. 96).

*Genus et species indet.

Material: 5 specimens; identified by A. Jerzmańska as *Apostasis* sp. Specimens transferred to the family Acanthuridae (Genus et species indet.) in 1989, following A. Bannikov's suggestion.

Comments – Acanthuroidei: 1 family: Acanthuridae (6); 1 genus, 1 unidentified form. Number of specimens in the collection: 6.

Suborder SPHYRAENOIDEI Starks, 1899

Family SPHYRAENIDAE Rafinesque, 1815

Genus *Sphyraena* Röse, 1793

Sphyraena sp.

Material: 1 specimen; identified to the level of genus *Sphyraena*.
Comments – Sphyraenoidei: 1 family: Sphyraenidae, 1 genus *Sphyraena*. Number of specimens in the collection: 1.

Suborder SCOMBROIDEI Bleeker, 1859

Family EUZAPHLEGIDAE Daniltshenko, 1960

Genus *Palimphyes* Agassiz, 1844

Palimphyes lanceolata (Simionescu, 1905)

Material: 1 specimen; identified to the level of species; undescribed.

Palimphyes sp.

Material: 106 specimens; classified with the joint group *Palimphyes*; including: described as *Palimphyes* sp. (7) (Jerzmańska, 1968; p. 460); undescribed (99). Jerzmańska (1968; p. 461) suggested that several species of the genus *Palimphyes* exist in the Polish Carpathians.

Family GEMPYLIDAE Goode et Bean, 1895

Genus *Hemithyrsites* Sauvage, 1873

Hemithyrsites rumanus (Jonet, 1958)

Material: 2 specimens; identified to the level of species (Jerzmańska & Kotlarczyk, 1975; p. 881).

Hemithyrsites sp.

Material: 71 specimens; classified with the joint group *Hemithyrsites*; some specimens identified as *Hemithyrsites* sp.

Genus *Thyrstitoides* Fowler, 1929

Thyrstitoides sp.

Material: 39 specimens; classified with the joint group *Thyrstitoides*; some specimens identified as *Thyrstitoides* sp.; in biostratigraphical works indicated as *Thyrstitoides zarathoustrae* Arambourg, 1967 (e.g., Jerzmańska & Kotlarczyk, 1975; p. 881).

*Genus et species indet.

Material: 356 specimens; identified to the level of family Gempylidae; including: specimens described (22); undescribed (334).

Family TRICHIURIDAE Rafinesque, 1810

Genus *Lepidopus* Gouan, 1770

Lepidopus glarisianus (Blainville, 1818)

Material: 93 specimens; including: described as *L. glarisianus* (93) (Jerzmańska, 1968; p. 463). Basing on osteological analysis of 70 specimens of *Lepidopus*, M. Żabrowski changed the generic name *Lepidopus* to *Anenchelum* (Żabrowski, unpublished Ph.D. thesis, 2004). Bannikov and Parin (1995; p. 183–192) provided reasons for restoration of the genus *Anenchelum*.

Lepidopus isopleurus (Agassiz, 1834)

Material: 11 specimens; identified to the level of species; including: specimens described as *L. isopleurus* (5) (Jerzmańska & Kotlarczyk, 1975; p. 881); undescribed (6). Basing on osteological revision of *Lepidopus isopleurus* (Agassiz, 1834), M. Żabrowski shifts these specimens to a created by himself species *Lepidopus jermanskae* (Żabrowski, unpublished Ph.D. thesis, 2004).

Lepidopus sp.

Material: 800 specimens; classified with the joint group *Lepidopus*; some specimens identified to the level of genus *Lepidopus*; including: specimens described as *Lepidopus* sp. (16); mentioned (7); undescribed (476).

*Genus et species indet.

Material: 10 specimens; identified to the level of family Trichiuridae.

Family PALAEOORHYNCHIDAE Günther, 1880

Genus *Palaeorhynchus* Blainville, 1818

Palaeorhynchus sp.

Material: 124 specimens; classified with the joint group *Palaeorhynchus*; including: specimens described as *Palaeorhynchus* sp. (1) (Jerzmańska, 1968; p. 466); undescribed (123); fragments of skeletons; mostly isolated bones.

Genus *Pseudotetrapturus* Daniltshenko, 1960

**Pseudotetrapturus* sp.

Comment: no specimens identified as *Pseudotetrapturus* sp. have been found. This taxon was mentioned in the lists compiled for the Polish Carpathians (Kotlarczyk, 1985, p. 56–57; Jerzmańska & Kotlarczyk, 1988, p. 104–105).

Family SCOMBRIDAE Rafinesque, 1815

Subfamily SCOMBRINAE Rafinesque, 1815

Genus *Scomber* Linnaeus, 1758

Scomber voitestii Paucă, 1929

Material: 11 specimens; including: described (3) (Jerzmańska,

1968; p. 466); undescribed (7); showing species' properties (Paučá, 1929a; p. 112).

Genus *Acanthocybium* Gill, 1862

Acanthocybium sp.

Material: 2 specimens; identified as *Acanthocybium* sp.

Genus *Sarda* Cuvier, 1829

Sarda sp.

Material: 10 specimens; including: described (3) (Jerzmańska, 1960, p. 404; Jerzmańska & Kotlarczyk, 1988, p. 104–105); undescribed (7).

Subfamily THUNNINAE Starks, 1910

*Genus et species indet.

Material: 2 specimens; identified as Thunninae (2). Change of name of the specimen identified as *Thunnus* sp. introduced by A. Jerzmańska.

*Genus et species indet. A

Material: 105 specimens; identified to the level of family Scombridae.

*Familia et genus indet.

Material: 52 specimens; identified to the level of suborder Scombroidei; including: specimens mentioned as Scombridae (2) (Jerzmańska *et al.*, 2001); undescribed (50).

Comments – Scombroidei: 5 families: Euzaphlegidae (107), Gempylidae (468), Trichiuridae (938), Palaeorhynchidae (124), Scombridae (130), Familia et genus indet. (52); 5 species, 7 genera, 6 unidentified forms. Nearly 10% of forms determined as Scombroidei bear descriptions, the remaining ones require revision. Number of specimens in the collection: 1,824.

Suborder STROMATEOIDEI Regan, 1929

Family NOMEIDAE Günther, 1860

Genus *Psenicubiceps* Daniltshenko, 1980

Psenicubiceps sp.

Material: 4 specimens; identified to the level of genus *Psenicubiceps*; description (Daniltshenko, 1980a; p. 167).

*Genus et species indet.

Material: 1 specimen; identified to the level of family Nomeidae.

Family STROMATEIDAE Rafinesque, 1810

Genus *Pinichthys* Bannikov, 1985

Pinichthys sp.

Material: 6 specimens; identified in 1989 by A. Bannikov as *Pinichthys* (information derived from specimen's label).

*Familia et genus indet.

Material: 9 specimens; determined as the suborder Stromateoidei.

*Familia et genus indet. (Giant III)

Material: 1 specimen; classified as a new form; informal name Stromateoidei (?) (Giant III) proposed by A. Jerzmańska in 1989. Comments – Stromateoidei: 2 families: Nomeidae (5), Stromateidae (6), Familia indet. (9), Familia indet. (Giant III) (1); 2 genera, 3 unidentified forms. Number of specimens in the collection: 21.

* Genus et species indet. A

Material: 5 specimens; classified with the suborder Trichiuroidei by A. Jerzmańska, are shifted to the suborder Scombroidei.

*Order PERCIFORMES Bleeker, 1859

*Suborder indet.

*Familia et genus indet A

Material: 91 specimens; classified with the order Perciformes.

*Familia *Incertae sedis*

*Genus et species indet. (à la, à la)

Material: 46 specimens; classified as a new form; informal name: Perciformes (à la, à la) proposed by A. Jerzmańska in the years 1989–1991 (incomplete descriptions and hand-made drawings by A. Jerzmańska).

Comments – Perciformes: 8/7 (?) suborders: Percoidei (904), Trachinoidei (207), Gobioidi (1), Acanthuroidei (6), Sphyraenoidei (1), Scombroidei (1824), Stromateoidei (21), ?Trichiuroidei (5); 20 families; 14 species, 23 genera, 17 unidentified forms. Number of specimens in the collection: 3,101.

Order PLEURONECTIFORMES Bleeker, 1859

Family PSETTODIDAE Regan, 1910

*Genus et species indet.

Material: 1 specimen; identified to the level of family Psettodidae.

*Familia et genus indet.

Material: 33 specimens; classified with the order Pleuronectiformes, mentioned in the lists of taxa since 1985.

Comments – Pleuronectiformes: 1 family: Psettodidae (1), Familia indet. (33); 2 unidentified forms. Number of specimens in the collection: 34.

Order TETRAODONTIFORMES Regan, 1929

Family TRIACANTHODIDAE Gill, 1862

Subfamily TRIACANTHODINAE Gill, 1862

Genus *Carpathospinosus* Tyler et Jerzmańska, Bannikov, Świdnicki, 1993

Carpathospinosus propheticus Tyler et Jerzmańska, Bannikov, Świdnicki, 1993

Material: 10 specimens, described (Tyler *et al.*, 1993). Holotype: ZPALWr A/3000; Przysietnica [PS₅]. 1993. *Carpathospinosus propheticus* nov. sp.; J. Tyler, A. Jerzmańska, A. Bannikov, J. Świdnicki, p. 12, figs: 11, 12, 13, 17, 18, 19.

Carpathospinosus sp.

Material: 13 specimens; identified to the level of genus *Carpathospinosus*; including: mentioned (10); undescribed (3).

Subfamily HOLLARDIINAE Gill, 1862

Genus *Prohollardia* Tyler et Jerzmańska, Bannikov, Świdnicki, 1993

Prohollardia avita Tyler et Jerzmańska, Bannikov, Świdnicki, 1993

Material: 3 specimens, described (Tyler *et al.*, 1993). Holotype: ZPALWr A/2096; Błażowa [B₁]. 1993. *Prohollardia avita* nov. sp.; J. Tyler, A. Jerzmańska, A. Bannikov, J. Świdnicki, p. 3, figs.: 1–3, 7–10.

Genus *Parahollandia* Fraser-Brunner, 1941

Parahollandia (?) sp.

Material: 4 specimens; identified as *Parahollandia* (?) sp. It cannot be excluded that the name shown on specimen's label has been erroneously given by A. Jerzmańska instead of *Prohollandia*.

*Genus et species indet.

Material: 4 specimens; identified to the level of family Triacanthodidae.

Family BALISTIDAE Rafinesque, 1810

Genus *Oligobalistes* Daniltshenko, 1960

Oligobalistes sp.

Material: 1 specimen; identified to the level of genus *Oligobalistes* (Daniltshenko, 1960; p.164).

Genus *Apostasis* Kramberger, 1891

Apostasis sp.

Material: 7 specimens; identified by A. Jerzmańska as *Apostasis* sp.; identification requires revision.

*Genus et species indet.

Material: 6 specimens; identified to the level of family Balistidae.

Family OSTRACIIDAE Rafinesque, 1810

Genus *Oligolactoria* Tyler et Gregorová, 1991

Oligolactoria bubiki Tyler et Gregorová, 1991

Material: 1 specimen; mentioned (Tyler & Gregorová, 1991; p. 3) as a paratype: ZPALWr Os/397; Książce [KN1]. 1991. *Oligolactoria bubiki* nov. sp.; J. Tyler et R. Gregorová, p. 3.

*Genus et species indet.

Material: 1 specimen; identified as Ostraciidae.

*Familia et genus indet.

Material: 6 specimens; classified with the order Tetraodontiformes.

Comments – Tetraodontiformes: 2 holotypes; 3 families: Triacanthodidae (36), Balistidae (19), Ostraciidae (2), Familia indet. (6); 3 species, 4 genera, 3 unidentified forms. Number of specimens in the collection: 58.

*Ordo et familia indet.

Teleostei: Genus indet.

Material: 440 specimens; included into the group: Teleostei: Genus indet.; no information about taxon's name. Undescribed owing to doubts related to determination of diagnostic features.

*Familia indet.

Teleostei: Genus indet. A

Material: 11 specimens; classified with the group.

*Familia indet.

Teleostei: Genus indet. P

Material: 1 specimen; described as: Teleostei: Genus indet. (P).
Comments – Teleostei: Genus indet.: (452) undescribed; grouped under three names: Teleostei: Genus indet. (440); Genus indet. A (11); Genus indet. P (1); no information about taxon name. This group of specimens includes also representatives of orders: Clupeiformes; Beryciformes; Myctophiformes, and Gadiformes.

VARIABILITY OF FOSSIL ASSEMBLAGES OF THE CARPATHIAN ICHTHYOFAUNA

Long-lasting exploration of ichthyofauna along continuous sections of the Menilite Formation in the northern segment of the Carpathians, ca. 400 km² large, has supplied abundant quantitative material that makes it possible to determine variability of ichthyofaunistic assemblages both in time and space. It is possible, of course, to consider only the variability of fossil fish assemblages which record – to an unknown degree – the variability of biocoenoses during a 20 million years-long interval in the Northern Tethys basin. Apart from abundance of taphocoenoses and the ubiquity of their occurrence within black, bituminous clayey-siliceous shales, more or less complete fish skeletons occur only in thin, frequently horizontally laminated shale layers, intercalated by much more thicker layers of not laminated shales of similar colour, or other strata (grey and green shales, siltstones, mudstones, sandstones, cherts, marls, cohesive mudflow deposits). Such an observation has also been confirmed by other authors (Bieńkowska, 2004).

Range of the studied variability

The applied methodology allows one to study vertical variability of the assemblages of taphocoenoses in the following cases:

1. inbetween neighbouring layers within one exposure,
2. among several exposures arranged stratigraphically in the section of the Menilite Formation or the entire Menilite-Krosno Series,
3. between stratigraphically successive sequences of exposures that contain one homogeneous assemblage of ichthyofauna and the sequences containing a different assemblage.

The horizontal variability can be analysed in case of:

1. assemblages occurring in characteristic chronohorizons (e.g., Jasło Limestones),
2. assemblages associated with clearly marked and continuous lithostratigraphic divisions like, for instance, the pair of the Dynów Marl and Kotów Chert members,
3. qualitatively similar fish assemblages among individual sections of the study area.

The shape of the studied portion of the Carpathians enables one to characterise the last type of variability principally across the Oligocene Carpathian basin, and rarely along its axis.

An analysis of the above-mentioned types of variability will serve ecostratigraphic purposes and will be conducted with a view to ichthyofaunistic zonation, reflecting its present-day recognition. Purely taphonomic problems will not be dealt with in this paper.

The lithology of fish-bearing strata, i.e., hard, compact limestones and massive marls or brittle, easily disintegrating shales, as well as extremely rare occurrence of well-exposed larger sedimentary surfaces prevent recognition of the variability of fish assemblages among individual laminae comprising one fish layer (such fine-scale temporal variation in taphonomy of fishes found in laminated fresh-

water diatomites was studied by Wilson, 1993). Taking into account very low rates of sedimentation of laminated pelagic sediments (a few millimetres per 1,000 years), it can easily be concluded that we lose a possibility of estimating the variability of ichthyofauna within time-intervals important for living organisms. On the other hand, it cannot be excluded that some of the laminated layers represent the uppermost divisions of turbiditic depositional sequences, or that individual pairs of laminae belong to deposits of highly diluted turbidity currents. In the first case, it is not possible to conclude about any variability throughout the section of a fish layer, whereas in the second one technical difficulties make it impossible to study differences among fish assemblages that could have been supplied by successive turbidity currents in unknown time intervals. Therefore, irrespectively of the origin of fish-bearing deposits, temporal variability of individual assemblages within a fish layer of Carpathian sections cannot be reconstructed at this moment. Perhaps future specialist studies will enable for such a reconstruction. For the time being, the highest level of resolution is provided by variability among individual fish layers.

Possible causes of variability of ichthyofaunistic assemblages

The reasons for variability within Carpathian ichthyofauna are diversified and frequently difficult to identify. A preliminary discussion of these problems is given in a paper by Jerzmańska and Kotlarczyk (1973). It should be mentioned at this place that the variability of fossil ichthyofauna is controlled by: factors affecting the biocoenosis, those influencing upon the taphocoenosis composition, as well as the number of specimens per sample.

From among the primary, life conditions one should take into account: physico-chemical properties of the environment (water temperature, salinity, gas content), geographic-geological conditions (basin depth, presence of sea currents, including upwellings and horizontal currents (incl. gyre currents), basin topography and its changes, formation of natural barriers, rate of sedimentation, density of suspended load), biological factors (breeding, mortality, migrations), as well as factors controlling the origin of local domination of individual species and genera.

The post-mortem conditions include: the influence of sea currents, including turbidity currents transporting fish remains (re-deposition of not disintegrated skeletons can also occur after fossilization, owing to submarine slumps, olistoliths, and other gravity flows), the rate of decay and fossilization of organic material, and the role of necrofags. The activity of the latter is controlled by: the presence of anoxic conditions within sediments, mineral and chemical composition of both bottom sediments and those covering the bodies, rates of formation of the overlying laminae, and others.

The occurrence of layers bearing nearly homogeneous assemblages can also result from abnormal causes of mortality, like episodic mass extinction of fish shoals. This type of mortality, however, does not affect changes in biocoenosis composition in a longer time interval, but brings about unexpected accumulation of fish skeletons.

From a longer time perspective, the variability of assemblages is largely stimulated by the course of evolutionary processes, like natural disappearance of species and appearance of new ones, and the rate of immigration of new forms from the Indo-Pacific area into the studied fragment of the Tethys.

When analyzing the variability of assemblages occurring within individual layers, one should take into account the influence

of statistical representativeness of the assemblage upon its qualitative composition. A small number of exploited specimens can bias the real composition of taphocoenosis of the studied layer. It happens all too often that such poorly representative samples bear – first of all – the most numerous taxa of a given taphocoenosis, although less numerous taxa can constitute a remarkable share as well.

To estimate the reliability of the studied collection, an estimation of representative samples had already been performed by Jerzmańska *et al.* (1973; p. 116). The calculations are based on an assumption that sampling without return (relevant to exploitation of the fauna) does not change the infinitely great population of fish skeletons occurring in the Menilite Formation. Therefore, to calculate the size of a representative sample, one can use a formula of independent sampling (which does not require the knowledge of the size of general population and its distribution parameters): $n = u_{\alpha}^2 / 4d^2$; where: u_{α} is the respective value of distribution variable $N(0,1)$ for a given confidence level $1-\alpha$, and d is the maximum possible estimation error of the structure index. At the confidence level equal to 0.95, one should exploit from the layer at least 96 specimens, so as the maximum possible estimation error will not exceed 10% and, respectively, 394 specimens to reduce this error to 5%. At the confidence level reduced to 0.90, one should extract at least 67 specimens so as not to exceed 10% error, and 269 specimens not to exceed 5% error level. Such numerous samples, however, could seldom be obtained due to both technical difficulties and low frequency of skeletons. Therefore, the presented below analyses of variability among individual layers are usually biased by greater errors.

The reasoning applied to calculation of the representative sample taken from a layer can be also applied to sampling of the entire exposure. Also in this case, the number of exposures representatively sampled at the known allowable error is lower than that of all studied exposures (40/208).

Methodology of representation of ichthyofaunal variability

For all types of the analysed variability, a uniform pattern and graphic representation of tables has been applied. The columns represent: individual layers (sometimes a few successive ones), exposures (sometimes groups of neighbouring exposures or maintaining similar position within adjoining sections), logs within individual zones, as well as ichthyofaunal zones arranged in a stratigraphic order. The rows, in turn, contain taxa subdivided into groups including: species and genera, families and subfamilies, orders and suborders, as well as taxa labelled as *genus indet.* Subclasses (Elasmobranchii) appear sporadically. The succession of taxa within each group depends on the order of appearance within individual columns, starting from the first one. In case of higher number of taxa occurring at the same time, they are listed alphabetically (and not systematically), so as to enable their easy location.

The number of taxa within individual columns are shown by 10 classes, marked by either lines of different thicknesses or other graphic symbols and hues of grey.

Variability of fish assemblages among individual layers

Fish exploration by the stratonomic method, i.e. bed by bed, enables for distinguishing profound changes in the as-

semblages of Carpathian ichthyofauna. The first ever application of such a method to Jamna Dolna (J) exposure made it possible to distinguish two different ecological assemblages occurring one above another, and provisionally called “bathypelagic” (below) and “neritic-sublittoral” (above) (Jerzmańska & Kotlarczyk, 1968).

We shall start our description of the first type of variability from this site. During many years after publication of the quoted paper, extensive exploration of the Jamna Dolna site has been conducted. Among a few tens of ichthyofauna-bearing layers, detailed exploration of 28 layers has been performed (Fig. 6). A few lithological units (labelled A–G, cf. Jerzmańska & Kotlarczyk, 1968) have been distinguished in the section. Individual layers have been numbered consecutively within every lithological unit. These units represent the following lithostratigraphic members: A–B – sub-Chert Shale Member including porcellanites, C – Kotów Chert Member, D – Dynów Marl Member (in an exposure situated within a cliff high above the stream bed, siliceous marls undergoing long-term weathering were transformed into soft, porous siliceous shales), E–G – Rudawka Tractionite Member (see Fig. 4: Ł–J). Due to difficulties in identification of particular layers after a few year-long break in exploitation, newly exploited specimens have been referred to easily indetifiable, separate lithological units A, B, C, E, and F. Layers labelled as D₁, D₂, and D₃, previously assigned to the Dynów Marl Member, should probably be included into unit E.

Table 4. (Jamna Dolna) portrays the occurrence of individual taxa within both the explored layers and entire lithological units. Three types of taxa can be distinguished. The first one includes taxa occurring from the lowest to the uppermost layers, like *Lepidopus glarisianus* and *Clupea sardinites*. The second one represents taxa occurring in the lower part of the exposure only and not passing into the layers present at the top of unit D. The third type, in turn, includes taxa occurring in the upper part of the exposure, starting from the top of unit D or from the lower part of unit E. Jerzmańska and Kotlarczyk (1968) documented that the boundary between the second and third types separates the “bathypelagic” and “neritic-sublittoral” fish assemblages.

The diagram shows that layers assigned to the top of unit D represent, irrespective of original lithology, a higher, i.e., “neritic-sublittoral” ecological assemblage, distinguished in the hitherto applied ecostratigraphic scheme as the IPM2 Zone. Table 4. clearly indicates that within homogeneous bathypelagic assemblage (units A–C) some taxa begin to appear at a certain height above the base of the exposure, whereas others, commonly occurring throughout the section, are absent from some layers. Such a picture can be explained by either too small sample size, or local, unimportant variability. In case of some taxa like, for instance, those of the genus *Centriscus*, the restriction of their occurrence to unit B and the lower part of unit C only appears to suggest that their range is shorter than that of the entire bathypelagic assemblage. Another interesting phenomenon is the content of layer E1. This layer, 10 mm thick, differs remarkably from the other ones by unusual number of specimens dominated by *Trachinus minutus* (with prevailing number of juvenile forms), accompanied by *Hipposygnathus neriti-*

cus and *Glossanodon musceli* (also represented by a high amount of juvenile forms).

Similarly detailed documentation of 24 exploited layers enables one to distinguish a sharp boundary between the “bathy-pelagic” and “neritic-sublittoral” assemblages at Wola Węgierska – WE (Fig. 4: BP). The taxa *Scopeloides* sp. and *Palimphyes* sp. disappear in layers H₇ and H₈ (WE_{bp}), whereas in higher situated layers H and H₁(WE_{up}), *Glossanodon* sp., *Trachinus* sp., and *Serranus* sp. appear (cf. Table 15). Also in this exposure, *Centriscus* sp. displays a slightly narrower range than the entire “bathy-pelagic” zone.

An analogous change of assemblages has been documented by the stratonomic method within single exposures at Kotów – KT (Fig. 4: L), Malawa – M₂ (Fig. 4: L), Straszdyłe – S₁–S_{1b} (Fig. 4: B, Fig. 6), and – possibly – Skopów – SK (Fig. 4: BP).

Variability of the neritic-sublittoral ichthyofaunal assemblage within a single exposure was already studied in the 1970s at Rogi – RO₁ (11 layers) and Równe – R₁ (4 layers). At Rogi (Fig. 4: R), successive layers of the exposure bear a similar assemblage of taxa of the neritic-sublittoral assemblage, although one layer (No. 6) contains extremely numerous specimens, and the successive layer No. 5 bears the highest number of taxa. The studies of homogeneity of the ichthyofaunal assemblage at this exposures were conducted by Kotlarczyk *et al.* (1975) using the Rodionov’s criterion, and revealed that statistically significant differences exist between layer assemblages 1–5 and 6–11, less clearly between layers 5 and 4. These boundaries reflect both the presence of the above layers, as well as hiatuses in the continuity of taxa. On the other hand, the assemblage of Równe proved to be homogeneous.

Another, very important boundary separating different ecological assemblages has been identified at Krępak IV (Fig. 4: K–HB, Fig. 6). The Rudawka Tractionite and Borek Nowy Sheet-like Shale (layers 1–3) members, as well as Krępak Green Shale Member (layers 4–5) have been sampled. Table 5, similar to the previous one, clearly shows the boundary between layers 1–3, including *Glossanodon* sp. and *Serranus* sp. taxa (known from units D–G at Jamna), and layer 4 which bears new taxa: *Bregmaceros filamentosus* and *Polyipnus brevis*. The overlying layers include: *Kotlarczykia bathybia*, *Idrissia* sp., *Bathyprius* sp., *Hemithysites* sp., and *Eomyctophum* sp. That part of the section includes as well the taxa identified in units A–C at Jamna, like: *Vinciguerria* sp., *Vinciguerria distincta*, and *Thyrsitoides* sp. The above boundary separates the neritic-sublittoral assemblage from the overlying bathy-pelagic one, which is called “the upper bathy-pelagic assemblage” (Jerzmańska, 1968). It should be noted that ecological differences between the assemblage known from layers 4–5 in respect to the lower one are also underlined by the presence of deep-water taxa that belong to families: Gonostomatidae and Sternoptychidae, (in the hitherto-existing scheme, this assemblage is distinguished as the IPM3 Zone). The table also shows that some of the taxa occur only in single layers of the upper bathypelagic assemblage. This phenomenon can be explained in a way similar to that applied to the Jamna section. A slightly different assemblage comprised in layer

5 probably represents another, younger assemblage of the upper bathypelagic assemblage. This assemblage does not contain taxa typical for the IPM3 Zone, but includes *Hemithyrsites* sp. taxon, occurring for the first time above the base of the Menilite Formation.

This younger assemblage has been sampled at Przysietnica PS₆₋₅ section (Fig. 4: PS. Fig. 6). The top part of this exposure is composed of layers 1–50 (numbered from the top downwards), called PS₅ exposure, whereas the bottom layers 52–60 belong to exposure PS₆. The PS₅₋₆ exposure is composed of interbedded, a few centimetres thick layers of clayey, greenish-grey and clayey brown shales. The top of PS₆ exposure bears three layers of laminated limestones of the Wujskie Limestone Horizon (WL), very strongly weathered and partly decalcified. The exposure represents a part of the Menilite Formation member, belonging to the Sub-silesian Unit. The sequence of similar lithofacies development has been distinguished in Moravia (Czech Republic) as the Štitbořice Member (Stranik, 1981). Fish assemblages have only been found in brown shales and the above-mentioned limestones. Numerous layers bear a wealth of taxa (cf. Table 6.), including those present throughout the entire exposure, and those that begin to appear only from layers 46–42, like: *Centriscus* sp., *Centriscus nov.* sp., and *Syngnathus* sp. – typus A, although individual taxa are absent from some of the layers. The subsequent occurrence of a rich assemblage in layer 42 probably results from more representative sampling of this layer (627 specimens) as compared to the other ones. The presence of new taxa in layers 46–40, including – apart from the above-mentioned ones – such rare species, as *Carpathospinosus* sp., including species *propheticus*, *Forcipiger* sp., *Oligobalistes* sp., *Onobrosmius* sp., *Parahollandia?* sp., and *Caprovesposus* sp. marks the occurrence of a new, hitherto-unrecognised ecological assemblage. A less numerous assemblage present at the base of exposure PS₆ reveals properties of a transitional assemblage, because it includes both the taxon typical for the IPM3 Zone, i.e. *Bregmaceros filamentosus*, and those typical of the younger assemblage: *Africentrum* sp., *Carpathospinosus propheticus*, and *Idrissia* sp. The entire assemblage from exposure PS₆₋₅ is fairly homogeneous, and has been distinguished in this paper as the IPM4A Zone. Similarly as at Jamna, exposure PS₅ bears a layer (no. 42) with strongly dominating one taxon, i.e., *Centriscus* sp. Specimens of this taxon, together with those of *Centriscus nov.* sp. make up 78% of the entire assemblage exploited from this layer.

A stratigraphically younger part of the Menilite Formation has been sampled, i.a., at Krępak, in adjoining exposures (from the base to the top): KI, KI_{1-1a}, KIII (Fig. 4: K-B, Fig. 6). KI represents a layer of the Jasło Limestone (JL), the remaining 8 layers are comprised in a shale-sandstone complex.

Basing on the picture recognised at earlier-described exposures, two important boundaries can be identified here, despite the lack of representative sampling of all the layers (cf. Table 7). The first boundary is marked by the upper range of *Polyipnus* cf. *sobniowiensis*, typical for the Jasło Limestones and IPM4 Zone, the second one is documented by the first appearance of *Carpathichthys polonicus*, consid-

ered by Jerzmańska and Kotlarczyk (1981) as the index taxon of the IPM5 Zone.

Exposure at Bachów-3 (BH₃) (Fig. 4: BR, Fig. 6) will illustrate difficulties in distinguishing zone boundaries within the upper bathy-pelagic assemblage. The lowermost layer listed in Table 8 occurs ca. 15 m above the Jasło Limestone chronohorizon. One should expect at this position ichthyofauna typical for the IPM5 Zone. Instead, within 0.5 m higher situated, well-sampled shale complex (A₁), one specimen of *Argyropelecus* sp., characteristic for the IPM6 Zone, has been found. On the other hand, *Carpathichthys* sp., numbering 14 specimens, occurs only in a few layers of a ca. 2-m-thick complex situated some 10 m higher. We are confronted here with either early appearance of *Argyropelecus* sp. within the IPM5 Zone or even below, or late appearance of *Carpathichthys* sp. already in the IPM6 Zone. Taking into account that the share of the most important taxa within the assemblage exploited from the upper part of exposure BH₃ (from layer 17 to the uppermost one) is definitely compatible with the share of respective taxa within the assemblage coming from the stratotype exposure of Zone 5 (exposure K_{III} at Krępak), the former option has to be applied. In this case, the position of the lower boundary of the IPM5 Zone at exposure BH₃ will require further studies (cf. chapter “A new attempt...”).

An analysis of the number of individual taxa at exposure BH₃ clearly depicts horizon A₁ that shows distinct domination of *Africentrum* sp., *Holocentroides* sp., and *Lepidopus* sp. over the remaining taxa.

Changes in ichthyofauna of the upper part of the Menilite Formation have been documented at section Krępak II. This section includes six exposures, numbered from the bottom upwards: KII_b, KII_e, KII₁, KII₃, KII₂, and KII (Fig. 4: K-HB, Fig. 5), wherefrom a few tens of layers have been sampled (Fig. 6). Table 9 comprises selected layers of exposure KII₃ only. A few taxa are ubiquitous, although with some gaps. These are: *Argyropelecus* sp., *Eomyctophum* sp., *Thyrstitoides* sp., and *Merluccius* sp. The distribution of taxa within layers of exposure KII₃ at Krępak clearly shows that the higher number of taxa depends on the number of exploited specimens. For instance, layer no. 40 includes 7 taxa per 8 specimens, whereas layer no. 30 comprises 45 taxa per 478 exploited individuals. A striking feature is the presence of *Argyropelecus* sp. at section Krępak II. This taxon appears in successive exposures up to the last layer at KII₂, being absent from the three sampled layers and the entire, youngest exposure KII (15 taxa per 98 specimens). Disappearance of this stratigraphically important taxon, also observed at other sections, marks the boundary between the IPM6 Zone and the newly established IPM7 Zone.

The changes in fish assemblages within the upper part of the Menilite Formation can be reconstructed in one of the most detailed sampled exposures, i.e. Bachów 1 (BH₁). This exposure, already described by Jerzmańska and Kotlarczyk (1975, Fig. 3: cf. Fig. 6), bears a numerous (N = 1,273) ichthyofaunal assemblage comprised in 8 layers (Table 10). Half of the layers (2a, 2, 2g, 1) have been sampled representatively enough to indicate the unexpected lack of taxa: *Hemithyrsites* sp. in layers 2 and 2g, or *Syngnathus* sp. in

the uppermost layer 1, despite the fact that the latter taxon survived until the final stage of the basin existence. This lack can probably be explained by periodical changes in the biocoenosis.

It is difficult to decide unequivocally whether the reliably documented lack of *Argyropelecus* sp. in the topmost layers of the exposure should be treated as the previously mentioned periodical gaps, or should it be associated with the final disappearance of this taxon from the basin, as shown by an analysis of successive layers of the section at Krępak II. However, taking into account small thickness (ca. 60 cm) of the complex devoid of *Argyropelecus* sp. and lack of data coming from the overlying beds, it has been accepted that insufficient evidence exists to consider the absence of this taxon as a reflection of its complete removal from the basin. Therefore, the entire ichthyofaunal assemblage collected from BH₁ exposure has been included into the *Argyropelecus* sp. assemblage, belonging to the IPM6 Zone.

Concluding remarks

A review of ichthyofaunal changes within the layers of stratigraphically arranged exposures makes it possible to draw several general conclusions and to determine preliminarily the character of changes of fish assemblages during the existence of the sedimentary basin.

1. Most of the taxa appear in the section in some layers only.
2. The changeable spectrum of taxa in individual layers is largely dependent on the number of exploited specimens.
3. The appearance of individual, stratigraphically important taxa within a layer does not depend on the number of specimens it contains. Some taxa appear even in samples numbering a few specimens only, whereas others do not occur even in samples embracing a few hundreds of specimens, like, e.g., *Palaeogadus simionescui* in layer E₁ at Jamna Dolna (at confidence level equal to 0.95, and 5% error), or *Carpathospinosus propheticus* in layer 42 at Przysietnica (PS_{6/5}) (confidence level 0.90, error 5%). In such cases, the presence of periodical disappearance of taxa should be related to either life or post-mortem changes in the assemblage; although accidental lack of a given taxon cannot be excluded at the accepted error.
4. The changes of ecological assemblages are two-fold: they proceed either rapidly between neighbouring layers, or gradually through a number of layers. The first type includes changes between the lower bathy-pelagic and neritic-sublittoral assemblages, and between the latter and the upper bathy-pelagic one. The second type is represented by changes occurring within the upper bathy-pelagic assemblage, e.g., between the IMP3 and IPM4A zones, or between IMP5 and IPM6 zones. These changes consist in gradual rebuilding of the assemblage and co-existence of infrequent specimens of some of the taxa characteristic for the neighbouring zones, like *Carpathichthys* sp., and *Argyropelecus* sp. in the lower part of IPM6 Zone, or *Bregmaceros filamentosus* and *Carpathospinosus propheticus* in the lower part of IPM4A Zone.

Variability of ichthyofaunal assemblages among exposures within a stratigraphic section

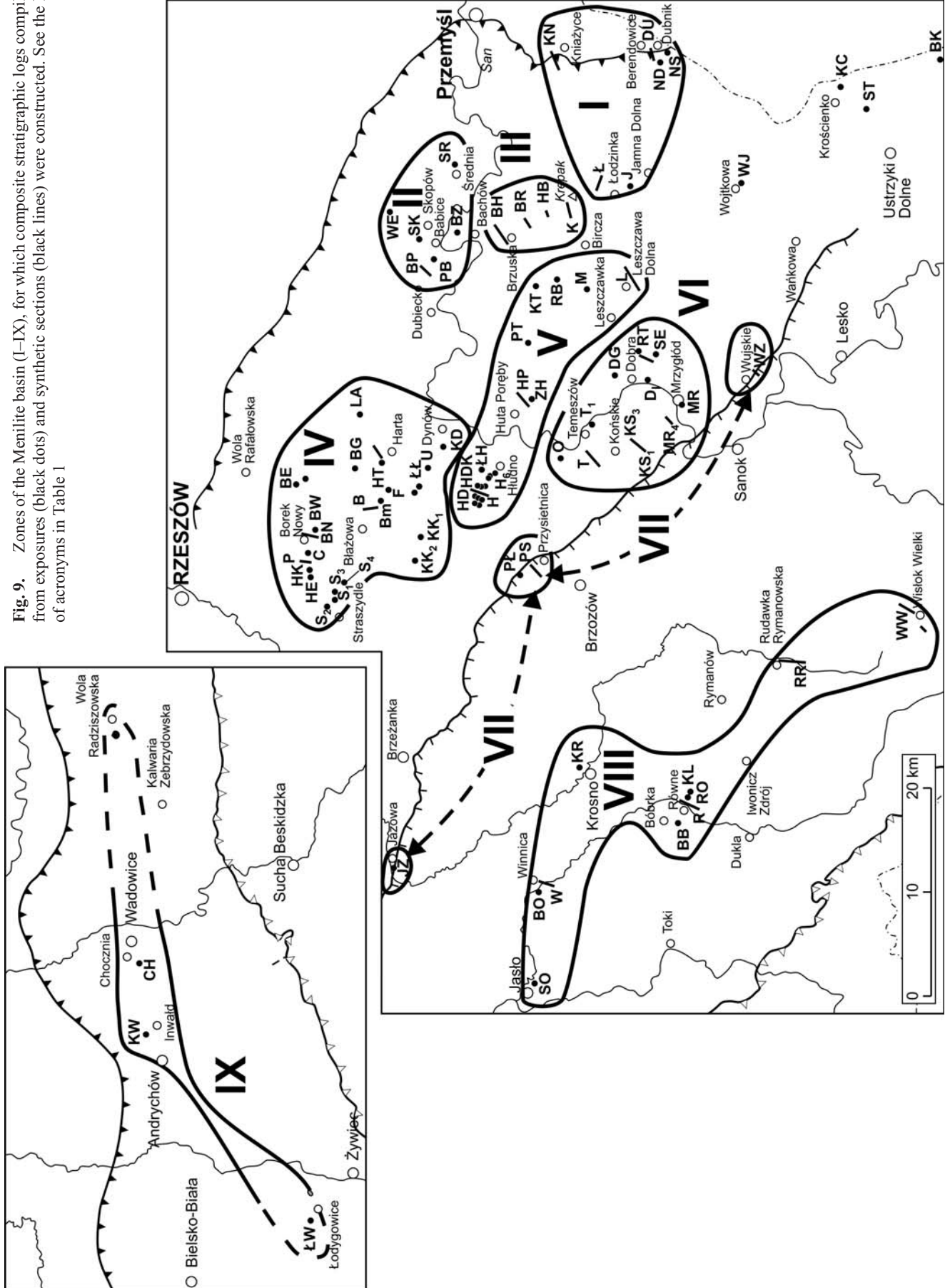
The most important problem of this paper is to characterise the nature of variability of ichthyofaunal assemblages in complete sequences of the Menilite Formation and, if at all possible, in the younger Krosno Formation. To achieve this task, it was necessary to collect and compare fish assemblages from stratigraphically arranged exposures for every section. Due to a number of reasons, it was very difficult to find the sufficient number of such exposures for a single section. Usually, the stratigraphic log was compiled from exposures occurring at several neighbouring partial sections. Therefore, stratigraphic arrangement of individual exposures required detailed geological mapping of the area, as well as taking into account correlative horizons. The mode of construction of such synthetic sections is described in "Methods", and the sections are shown on Fig. 4. Sometimes, palaeontological material comprised in synthetic sections appears to be insufficient, and their sampling incomplete. In such cases, data from two or more synthetic sections were combined into one composite section, being representative for a larger area, i.e., a basin zone. These zones are arranged chain-like, extending from marginal basin parts towards central parts, and some of these zones coincide – entirely or in part – with geological structures bearing exposures of the Menilite Formation. The following zones have been distinguished (cf. Fig. 9):

- I – between exposures of the Menilite Formation on the Carpathian margin up to Jamna Dolna and Łodzińska;
- II – between Wola Węgierska (WE) and Średnia up to Babice (this zone overlaps in part the inner part of the previous zone);
- III – the Menilite Formation stratotype area within the Brzuska-Krępak syncline (Krępak-Bachów zone);
- IV – between Borek Nowy - Brzezówka (BE) up to Straszydle, Błazowa, Kąkolówka (KK), and Łubno - Łazek (ŁŁ);
- V – between Leszczawa Dolna up to Hłudno, coinciding in part with the inner segment of the previous zone;
- VI – between Dobra and Temeszów up to Końskie and Mrzyglód;
- VII – Przysietnica, Jazowa and Wujskie;
- VIII – between Jasło and Krosno, and Bóbrka and Wisłok Wielki.

In addition, a section in the West Carpathians has been compiled basing on infrequent exposures close to Wadowice (IX).

It has to be noted that when analyzing variability among ichthyofaunal assemblages collected at exposures, we usually have at our disposal a greater number of individuals than that resulting from summing the respective numbers from individual layers. Some of these specimens could have been extracted from the exposure without describing their exact location in a given layer, or they could have been derived from heaps at the base of exposures, particularly those which have been exploited for many years. In some cases, additional taxa have been found at such locations, like e.g., *Eophycis* at Jamna Dolna. Such a way of collecting the material requires extreme care in case of exposures comprising

Fig. 9. Zones of the Menilite basin (I–IX), for which composite stratigraphic logs compiled from exposures (black dots) and synthetic sections (black lines) were constructed. See the list of acronyms in Table 1



two different ecological assemblages. This type of methodology is only accepted in stratigraphical works, and cannot be applied either in detailed reconstructions of local changes in ichthyofaunal assemblages, or in taphonomic studies.

We shall start our description of assemblage variability from the stratotype section, best documented and embracing the entire sequence of the Menilite Formation in the Brzuska syncline.

Composite section of the Krępak - Bachów zone (III)

This composite section has been constructed from two synthetic sections: Krępak - Huta Brzuska (Fig. 4: K-HB) and Brzuska - Bachów (Fig. 4: BR). This section includes 24 exposures selected from the following, continuous sections: Krępak (3 partial sections), Huta Brzuska (1 section), Brzuska (2 partial sections), Bachów (1 partial section). Data collected at exposures are summarised in Table 11 in 22 columns. In two cases, data from two exposures of small number of specimens have been combined. Similarly as in layer description, also in this case one can distinguish taxa occurring nearly continuously throughout all the exposures (these can be absent in case of poorly numerous samples), as well as taxa present in some exposures only, being usually represented by one specimen. The third group includes taxa associated with only one or few neighbouring exposures, and occurring only once in a section.

The first group embraces such common taxa, as: *Clupea* sp., *Eomyctophum* sp., *Lepidopus* sp., *Vinciguerrria* sp., or *Serranus* sp. Starting from exposure KIV₄₋₅, ubiquitous are: *Hemithyrssites* sp., *Idrissia* sp., and *Thyrssitoides* sp., whereas starting from exposure KI₁ *Africentrum* sp., *Merluccius* sp., and *Syngnathus* sp. are common. Beginning from exposure BH₃, *Argyropelecus* sp. begins to appear.

The second category includes *Eomyctophum* cf. *koraense*, *Priacanthus* sp., and *Scomber* *voitestii*.

The taxa restricted to one or few neighbouring exposures are represented by: *Scopeloides* sp. and *Scopeloides glarisianus* at the lowermost exposure KI₃; *Glossanodon musceli*, *Glossanodon* sp., and *Palaeogadus* sp. at exposures BR 43 and KIV₁₋₃; *Bregmaceros filamentosus*, *Kotlarczykia bathybia*, and *Polyipnus brevis* at exposure KIV₄₋₅; *Polyipnus sobniowiensis* at KI; *Carpathichthys polonicus* and *Carpathichthys* sp. at KIII, HB₆, and BH₃; *Syngnathus* sp.-typus A, *Centriscus* sp. and others at BH₃. Rare and only once occurring taxa include, i.a., *Paraberyx bachoviensis* and *Lepidopus isopleurus* at exposure BH₁, *Glyptophidium* sp., *Onobrosmius* sp., *Palaeogadus intergerinus*, *Capros medianus* at exposure KII₃, and *Eomyctophum menneri* at KII. The presence of taxa occurring exclusively in a given position of the section provides a good opportunity for stratigraphic zonation, provided that similar succession of taxa is repeated in other sections.

The described composite section is characterised by domination of some of the taxa at individual exposures. For instance, at exposure BH₃ dominant are: *Africentrum* sp., *Lepidopus* sp., and *Eomyctophum* cf. *koraense*; exposure BH₁ is dominated by *Syngnathus* sp., *Eomyctophum* sp., *Clupea* sp., and *Lepidopus* sp., whereas exposure KII₃ is dominated by *Argyropelecus* sp., accompanied by *Eomycto-*

phum sp. and *Clupea* sp. It should be remarked at this place that the unusual dominance of *Argyropelecus* sp. at exposure KII₃ is associated with exceptional large number of specimens of this taxon in layer no. 30, and that strong dominance of *Syngnathus* sp. at exposure BH₁ is related to a high percentage of this taxon in four neighbouring layers (3–2g), situated within a 0.5 m thick complex.

Composite section of the Błażowa - Borek Nowy zone (IV)

This area is shifted towards the NW in respect to the axis of the main cross-section transecting the majority of zones (Fig. 9).

Data listed in Table 12 have been derived from 41 exposures (cf. two synthetic sections of this zone in Fig. 4: B, BN), and assemblages collected at some exposures of the same lithostratigraphic member, particularly less numerous ones, have been combined like, e.g., those of the Dynów Marls at Błażowa -Walant (BW), and of an olistolith of the latter at Hermanowa - Kamieniec (HK₂). The data are presented in 24 columns. Column KK₁ represents an exposure of the sub-Chert beds at Kałokolówka (Fig. 6). The next 6 columns portray fish assemblages from the Kotów Marl and Dynów Marl members, whereas columns S₃-S_{1b} to B_m represent assemblages of the Rudawka Tractionite, Futoma Diatomite, and Borek Nowy Sheet-like Shale members. Columns ŁŁ₁ and BN₇-BG represent the Jasło Limestone Horizon, and columns B₁ through B₁₅ illustrate the composition of fish assemblages of the younger (supra-Jasło) part of the Menilite Formation, mainly the Błażowa Mbr. Column HT portrays an assemblage of the Krosno Formation at Harta exposure.

The first group of taxa listed in the table (species and genera) clearly shows boundaries between those assemblages wherein new taxa appear and older ones disappear. At exposures KK₁ through ŁŁ₂ there appear and commonly occur such taxa, as: *Scopeloides* sp., *Palimphyes* sp., *Eomyctophum limicola*, and *Cetorhinus* sp., whereas *Centriscus henrichi*, *Centriscus teleajensis*, *Vinciguerrria talgiensis*, *Barbus* sp. and others occur sporadically. These taxa do not pass into higher-situated exposures (S₃ through B_m), being replaced by: *Holosteus* sp., *Ammodytes* sp., and *Capros* sp., whereas *Glossanodon* sp., found only at exposures S₁ and S₂ at the top of the Dynów Marl, maintains its ubiquitous presence. These taxa do not occur in exposures representing a younger part of the Menilite Formation of this zone.

Exposures of the Jasło Limestones (here mainly at ŁŁ₁) bear, nearly exclusively, a new assemblage with *Eomyctophum* cf. *koraense*, *Eomyctophum menneri*, *Idrissia carpathica*, *Idrissia* sp., and *Holocentroides moldavicus*. The taxa of *Polyipnus sobniowiensis*, *Polyipnus* sp., and *Priacanthus longispinus*, as well as a shark *Alopecias* are confined exclusively to the limestones.

Another group of four exposures (B₁ through B₄) of the Menilite shales intercalated by Kliwa sandstones, situated one upon another in a continuous section at Błażowa, displays ubiquitous occurrence of *Argyropelecus* sp., as well as the appearance and disappearance of: *Palaeogadus distinctus*, *Palaeogadus intergerinus*, *Prohollandia avita*, *Proto-*

myctophum sp., *Psenicubiceps* sp., *Argyropelecus cosmovi-*
cii, *Capros medianus*, *Propteridium* sp., *Parahollandia?*
sp., and others. Of special importance is the occurrence at
exposure B₄, apart from *Argyropelecus* sp., of representa-
tives of deep-water families Ceratiidae and Alepocephali-
dae. Another group of exposures (BE₂ to B₁₅) of the highest
part of the Menilite Formation displays remarkable decrease
of the assemblages, where most of the previously described
taxa do not occur. This impoverished assemblage is domi-
nated by *Eomyctophum* sp., *Vinciguerrria* sp., and *Merluc-*
cius sp., and – first of all – *Syngnathus* sp.

The last individualised group of taxa can be examined
at Harta. There occur for the first time: fairly numerous
Leiognathus cf. *minutus*, as well as *Merluccius hartensis*,
Merluccius errans, and *Caranx gracilis*, whereas *Syng-*
nathus sp. and *Lepidopus* sp. continue to exist, and *Clupea*
sp. flourishes.

The described zone does not contain numerous, clearly
dominating taxa. Infrequent exceptions are represented by
fairly numerous *Scopeloides* sp. at exposures S₁ + S₂ (55),
Eomyctophum sp. at B₄ (136), and *Clupea* at Harta (75).

Assemblages with *Polyipnus brevis* and *Carpathichthys*
polonicus have not been found, despite extensive explora-
tion of numerous exposures in this zone.

Composite section of the Leszczawa - Kotów - Hłudno zone (V)

This section was constructed from synthetic Leszczawa
and Hłudno sections (Fig. 4: L, H). Twenty-five exposures
(Fig. 9) are arranged into 15 columns by combining, as pre-
viously, less numerous fish assemblages from exposures be-
longing to the same lithostratigraphic member (Table 13).

The first two columns comprise data derived from ex-
posures that represent the Kotów Chert and Dynów Marl
members. Only these exposures do contain exclusively such
taxa, as: *Centriscus* sp., *Centriscus longispinus*, *Centriscus*
heinrichi, *Cetorhinus* sp., *Eomyctophum limicola*, *Palim-*
phyes sp., and *Vinciguerrria talgiensis*. The next four col-
umns clearly show a group of exposures belonging to the
Rudawka Tractionite Member. There only occur: *Glossano-*
don sp., *Glossanodon musceli*, *Palaeogadus* sp., and *Serra-*
nus budensis, whereas some of exposures contain as well
single or infrequent specimens of *Eophycis jamnensis*, *Eo-*
phycis sp. and *Trachinus minutus* (at L), *Holosteus* sp. (at
M₂), *Hemiramphus jerzyi* (at RB₃), and others.

At exposure L 1, stratigraphically higher than exposure
L at Leszczawa, there occurs a pair of taxa: *Kotlarczykia*
bathybia and *Polyipnus brevis*, unknown from other expo-
sures, as well as a single *Mugil* sp., and others.

The next column (H₁₁₉, KC₁) represents the Jasło
Limestone Horizon that was sampled at Hłudno and, addi-
tionally, at Krościenko on the Strwiąż River outside the de-
scribed zone, although in the same structure as Hłudno (cf.
Fig. 1). *Polyipnus sobniowiensis* is a characteristic taxon for
these exposures.

The assemblage from the successive column (exposures
H₁ – H₇) is the only one within the entire section which
bears *Argyropelecus* sp.

The two next columns HD₃-HD₁ are characterised by
the presence of single specimens of rarely occurring taxa,
including that of a shark *Notidanus*, as well as the increased
amount of *Syngnathus* sp. and *Merluccius* sp., and excep-
tionally strong dominance (in HD₁) of *Eomyctophum* sp.
and *Clupea* sp. It is worth noting that, despite the presence
of representative sample (217 specimens, including 127
within one layer), no traces of *Argyropelecus* sp. have been
found in exposure HD₁ (Fig. 6).

Columns representing exposures HDK and ŁH₁ - ŁH₂
(their position in the section is, however, uncertain due to
tectonic complications) portray a composition partly similar
to the two previous ones, although both qualitatively and
quantitatively impoverished.

Exposures listed in the last two columns represent the
Krosno Formation, displaying even smaller number of taxa.
In such a case, of special importance is the occurrence at
Huta Poręba (HP) exposure only, i.e., in the lower part of
the Leszczawka Diatomite Member (cf. Fig. 6), of *Merluc-*
cius errans, apart from still persisting in the basin taxa of
Merluccius sp. and *Syngnathus* sp. It should also be men-
tioned that close to another exposure at this locality, in the
Zahuty (ZH) stream bed, one specimen of *Caranx gracilis*
(Kotlarczyk, 1966) has been found. This specimen, how-
ever, was not included into the collection under study.

The analysed set of exposures has not provided data
pertaining to the *Carpathichthys polonicus* assemblage.

Composite section of the Dobra - Temeszów - Mrzygłód zone (VI)

Exposures of the Menilite and Krosno formations in
this zone represent the innermost part of the Skole Unit (cf.
Fig. 9). Its composite section has been compiled from the
Temeszów and Mrzygłód – Końskie synthetic sections (Fig.
4: T, MR-KS). Ichthyofauna was exploited at 16 exposures,
but only four of them provided more numerous samples
(O₂, T₁, DG, D₁). Therefore, some of the exposures which
were less representatively sampled but attained comparable
position in the log of the Menilite-Krosno Series in one or
two adjoining geological structures, were treated together
and presented in nine columns (Table 14).

At exposure Obarzym 2 (O₂) representing the Kotów
Chert Member and the lower part of the Dynów Marl Mem-
ber there occur *Scopeloides* sp., *Cetorhinus* sp., and *Vin-*
ciguerrria sp., which are absent from stratigraphically
higher-situated exposures. The three next columns (expo-
sures) represent the Rudawka Tractionite Member, and bear
– occurring exclusively herein – *Glossanodon* sp., *Glossa-*
nodon musceli, *Palaeogadus* sp., *Palaeogadus simionescui*,
and *Serranus budensis* (dominating at DG), as well as spo-
radically occurring *Properca* sp., *Pinichtys* sp., *Sarda* sp.,
and *Caranx petrodavae*.

The following column (MR₁ – T₄) represents the Jasło
Limestone Horizon at two exposures. *Polyipnus sobniowi-*
ensis and *Eomyctophum* cf. *koraense* appear only here. Ex-
posures situated not high above the Jasło Limestones (MR₂,
MR₃, T₂) (cf. Fig. 4: MR-KS, T) bear a poor and not signifi-
cant assemblage.

The next column combines assemblages derived from a few exposures situated at a similar position within the log of the Menilite Formation at Siemowica (SE_{1,2,3}) and Temeszów (T₃). Only in this assemblage (but exclusively at SE₃) does occur *Carpathichthys polonicus*, with important share of more common taxa, such as *Africentrum* sp. and *Holocentroides moldavicus*.

The second to last column includes exposures of the upper part of the Menilite Formation where, similarly as at Bachów 1, intercalations of cherts within shales do appear (cf. Fig. 4: MR-KS). The most characteristic taxon is *Argyropelecus* sp.

The final column represents the uppermost intercalation of Menilite shales, already within the Krosno Formation. A solitary specimen of *Syngnathus* sp. has been found here.

In the composite section of this zone, the *Polyipnus brevis*-bearing assemblage has not been found.

In the following part of this chapter, sections representing the zones situated outside the stratotype Kępak area will be discussed proceeding towards the Carpathian margin.

Section of the Babice, Wola Węgierska - Średnia zone (II)

In this zone only 7 exposures have been sampled (cf. Fig. 9, Fig. 4: BP), wherefrom one, at Wola Węgierska, embraces two different ecological zones, similarly as at Jamna Dolna. Therefore, it has been subdivided into two parts, the lower and upper ones. On the other hand, assemblages derived from closely-spaced exposures of the same outcrop of Menilite strata: Babice – Połanki 1 (BP₁) and Bachów Zadworze (BZ) have been combined (Table 15).

The lower part of Wola Węgierska exposure (N = 175) and well known historical exposure at Skopów (N = 257) (Rychlicki, 1909), including the Kotów Chert Member and poorly developed Dynów Marl Member, are characterised by the occurrence of: *Centriscus* sp., *Centriscus longispinus*, *Palimphyes* sp., and *Palaeorhynchus* sp., *Scopeloides* sp. appears exclusively at Wola Węgierska, whereas at Skopów only there occur *Scopeloides glarisianus*, *Centriscus heinrichi*, and *Centriscus teleajensis*, as well as a rare genus *Diaphus* sp. These taxa do not pass into the higher situated group of exposures (columns: WE upper part, N = 140, BP₁ + BZ and SR) that represent the Rudawka Tractionite Member and, in part (at WE), the Futoma Diatomite Member. Associated exclusively with this group are: *Serranus* sp., *Serranus budensis*, *Palaeogadus* sp., and *Palaeogadus simionescui*, whereas solitary specimens include *Eophycis* sp., *Capros* sp., *Palaeomolva* sp., and *Trachinus?* sp.

A numerous assemblage (N = 207) at Babice - Połanki – 2 (BP₂) is characterised by exclusive occurrence of *Argyropelecus cosmovicii*, *Argyropelecus* sp., *Eomyctophum* cf. *koraense*, *Eomyctophum menneri*, and *Syngnathus incompletus*, as well as the appearance of rare taxa, like: *Glyptophidium* sp., *Palaeogadus distinctus*, *Palaeogadus intergerinus*, *Parasteindachneria oligocaenica*, and *Syngnathus* sp. typus A., apart from commonly occurring within the upper bathy-pelagic assemblage: *Africentrum* sp., *Hemithyr-sites* sp., and *Thyr-sitoides* sp.

The uppermost exposure of the Przedmieście Babickie

(PB) section, shortly below the Krosno Formation, reveals a strongly impoverished assemblage at a lower number of specimens (N = 27). The lack of *Argyropelecus* is important. In the analysed zone no exposures representing assemblages of the IMP3 through IPM5 zones have been found.

Composite section of the Jamna Dolna, Łodzinka - Carpathian margin zone (I)

This zone includes both exposures at Jamna Dolna and Łodzinka (situated close to the Kępak zone), and those situated in the outermost slice of the Flysch Carpathians at Książyce and Dubnik; totally numbering 11 exposures (cf. Fig. 9, Fig. 4: Ł-J, KN, DU).

Exposure at Jamna Dolna has been subdivided into two parts representing different ecological members. The lower part (J_{A-C}, N = 231) includes the sub-chert shales from Jamna Dolna Member and the Kotów Chert Member. This part of the section is characterised by exclusive occurrence of *Scopeloides* sp., *Scopeloides glarisianus*, and *Palimphyes* sp. taxa, all species of the genus *Centriscus* sp., as well as: *Capros radobojanus*, *Eomyctophum limicola*, *Cetorhinus* sp., *Vinciguerria obscura*, *Vinciguerria distincta*, and other taxa (Table 16).

The upper part (J_{D-G}, N = 571), including the Rudawka Tractionite Member and the highest part of the Dynów Mbr, is characterised best by taxa which do not reappear elsewhere: *Glossanodon musceli*, *Palaeogadus simionescui*, *Hipposyngnathus neriticus*, *Trachinus minutus*, *Trachinus* sp., *Eophycis jamnensis*, and others.

Situated higher up in the section of the Menilite Formation three exposures: Ł₂, KN₄, and DU₄ supplied infrequent fossils, bearing taxa typical of the upper bathy-pelagic assemblage: *Eomyctophum* cf. *koraense* and *Forcipiger* sp. (very rare species). Taking into account the position of these exposures below the Jasło Limestone Horizon, the above assemblage can represent the IPM4A Zone.

The next four exposures (KN₁, DU₃, Ł₁, Ł_{1A}) are associated with the Jasło Limestone Horizon. An important feature is the lack of *Polyipnus sobniowiensis*, a taxon characteristic of this horizon. Among new taxa, one should list *Eomyctophum menneri* and rare *Oligolactoria bubiki*.

Two successive exposures of a higher part of the Menilite Formation bear solitary specimens of poorly characteristic taxa, whereas the uppermost exposure of his section (DU₁) includes the only taxon of *Syngnathus* sp., similarly as in the Temeszów – Mrzygłód zone.

The composite section of this zone provides pieces of unquestionable evidence only for the occurrence of three basic ecological assemblages of ichthyofauna. The exposure at Jamna Dolna represents the stratotype for the two lower assemblages.

Section of the Przysietnica zone (VII)

The section at Przysietnica (Fig. 9) represents the Sub-silesian Unit that shows a different facies development of the Menilite Formation. The lower part of this formation includes thin and poorly marked Kotów Chert, Dynów Marl, Rudawka Tractionite, and Borek Nowy Sheet-like Shale members which, however, have not been sampled (Fig. 4: PS).

The upper part of the section is usually devoid of sandstones, being composed of intercalated brown and greenish-grey shales. Eleven exposures bearing fish fossils are situated in this part of the formation which builds at least two tectonic slices (Fig. 4: PS). The most important exposures are arranged in a stratigraphic order in Table 17.

The position of exposure PS0 within the section has been established in a rough way only. Its location was neither positioned precisely in an earlier paper (Jerzmańska, 1968), nor verified during subsequent stratigraphical works.

The exploited material is not always representative because only few exposures (PS₆₊₅, PS₇, PS₈) provided a larger number of specimens (resp.: 1511, 402, and 437). Only the lowermost exposure of this set (PS₇) does include: *Polyipnus brevis*, *Kotlarczykia bathybia*, *Kotlarczykia* sp., *Bregmaceros filamentosus* and *Bregmaceros* sp., and a few poorly characteristic taxa represented by solitary specimens.

Bregmaceros filamentosus and *Bregmaceros* sp. pass into the higher situated exposure PS₆₊₅ which originated due to linking by a ditch of exposures PS₆ and PS₅. This exposure includes a differentiated set of taxa which appear in large or significant numbers of specimens exclusively in this position of the Przysietnica section. These are: *Centriscus* sp., *Centriscus* nov. sp., *Carpathospinosus* sp., *Carpathospinosus propheticus*, as well as such rare taxa, like: *Caprovesposus* sp., *Forcipiger* sp., *Oligobalistes* sp., *Onobrosmius* sp., and *Parahollandia* ? sp. There also occur more common taxa, e.g., *Holosteus* sp., *Fistularia* sp., and others. Dominance of *Centriscus* sp. is associated with the "Centriscus layer", already mentioned in the previous chapter. Significantly frequent are also: *Clupea* sp., *Lepidopus* sp., *Palaeorhynchus* sp., *Syngnathus* sp., *Antigonia* sp., *Centriscus* nov. sp., and *Syngnathus* sp. - typus A.

The PS₆₊₅ ichthyofaunal assemblage, significantly different from all the above discussed assemblages of the Skole Unit, should be distinguished as a separate Zone IP-M4A.

The next two exposures PS₃ and PS₂, shown in one column in Table 17, represent the Jasło Limestone Horizon. A characteristic taxon, exclusive for this horizon, is *Polyipnus* cf. *sobniowiensis*.

The next column shows composition of the ichthyofaunal assemblage of exposure PSO. A striking feature here is the co-occurrence of *Argyropelecus* sp. (one specimen) and *Carpathichthys polonicus* (1 specimen). Most probably, exposure PSO represents that segment of the Menilite Fm. which extends from the Jasło Limestone Horizon (wherein no index taxon has been found) up to the lower layers of Zone IPM5. Hence, this segment would mainly embrace strata coeval with those of exposure K I_{1+1a} at Krępak, and the lower part of exposure BH₃ at Bachów. The latter include a single specimen of *Argylopelecus* sp.

The two following columns, representing exposures PS₁ and higher situated PS₁₀, supplied poor ichthyofauna. Nevertheless, the clear presence (5 individuals per 7 specimens) of *Argyropelecus* sp. (at PS₁₀), representatives of the family Alepocephalidae, and the unknown from elsewhere taxon *Syngnathus* sp. typus B (at PS₁) is significant.

Exposure PS₈, belonging to the lower slice, maintains a stratigraphic position similar to that of PS₁₀. There occur numerous specimens of such characteristic taxa, as: *Argyropelecus* sp., *Merluccius* sp., and *Syngnathus incompletus*; less frequent are: *Palaeogadus distinctus* and *Parasteidachneria oligocenica*, as well as rare *Glyptophidium* sp. However, dominant components of the assemblage are common taxa, like: *Eomyctophum* sp. and *Clupea* sp.; accompanied by a considerable amount of *Lepidopus* sp. The sampled, higher part of the Menilite Fm. section at Przysietnica does not reveal the IPM5 Zone only (perhaps it appears at exposure PS₁), whereas that part of the section which contains exposures PS_{6,5} and PS₄ (cf. Fig. 4: PS) has been considered as the IPM4A Zone stratotype.

Composite section of the Jasło - Krosno - Wisłok Wielki zone (VIII)

Only one section at Wisłok Wielki (Fig. 4: WW) does represent the Dukla Unit, the remaining exposures belong the Silesian Unit (Fig. 9, Fig. 4: RR, R, W). Ichthyofauna was collected at 18 exposures of the Menilite Formation and at one exposure of the Jasło Limestone (SO). The latter is already situated within the Krosno Formation (Fig. 4: W).

Exposures at Rudawka Rymanowska (RR), Rogi (RO), Brzozówka (BO), and Krosno (KR) from the first four columns of Table 18 represent the lowermost part of the Menilite Formation (the thin Kotów Chert and Dynów Marl members; cf. Fig. 4). These exposures bear an uniform, although poor assemblage of taxa, from which *Scopeloides* sp. and *Cetorhinus* sp. do not appear up the section. To the same assemblage one can include specimens of *Centriscus heinrichi*, found earlier at Bóbrka and Lubatówka, and described by Böhm (1941).

The next group of exposures (from RR₁₋₃ to W) represents the entire remaining, upper part of the Menilite Formation in Silesian Unit, undivided into members, and composed mainly of shales, siltstones, and less frequent thin-bedded sandstones. Variability of the qualitative spectrum of ichthyofaunal assemblages, analysed among the exposures, appears to depend on the number of exploited specimens per exposure. The contrasting end-members are represented by exposures at Rogi (RO₁ – 528 specimens, 17 taxa) and Winnica (W – 139 specimens, 11 taxa), as well as Klawiec (KL – 16 specimens, 6 taxa) and Bóbrka (BB – 10 specimens, 4 taxa). Exclusively this group of exposures includes taxa: *Serranus budensis*, *Serranus* sp., *Glossanodon musceli*, *Glossanodon* sp., *Palaeogadus simionescui*, and rare: *Scomber voitsetii*, *Capros radobojanus*, *Caranx petrodavae*, *Eophycis jamnesis*, *Holosteus mariae*, *Hemiramphus jerzyi*, *Syngnathus incompletus*, and *Trachinus* ? sp.

It is important to note that none of numerous taxa characteristic of the upper bathypelagic assemblage, recognised in the Skole and Subsilesian Units, have been found within the Menilite Formation of the VIII zone. These taxa appear in the Jasło Limestone Horizon only. At Sobniów near Jasło (SO), a rich assemblage has been found, including typical for the Jasło Shales *Polyipnus sobniowiensis*, and known from the upper bathy-pelagic assemblage: *Eomyctophum* cf. *koraense*, *Eomyctophum menneri*, *Idrissia carpathica*, *Afri-centrum* sp., *Hemithyrssites* sp., and others. The difference

between this assemblage (column SO) and the lower, neritic-sublittoral one (column IPM2/Ó₂) is clearly marked in Table 18.

Composite section of the Wadowice - Żywiec zone (IX)

In the Western Carpathians, data coming from several exposures (Fig. 9) are available, including those of two sites described in previous papers. It was possible to verify some of the taxa (cf. Jerzmańska, 1968), particularly those from Krakowica near Inwałd, described by Heckel (1850), and from Wola Radziszowska, described by Kramberger (1879) (cf. Fig. 9).

Exposure at Krakowica (KW*), listed first in the Table 19 and well known from the existing literature, includes *Centriscus heinrichi*, typical of the chert member, and *Lepidopus glarisianus* (revision by Böhm, 1941). An exposure of cherts, probably that exploited by Heckel, has been found at a place called Krakowica (cf. Fig. 4: KW).

Two successive exposures at Choczniia (CH) and Krakowica (KW) (Fig. 4: CH, KW) include, i.a., an important taxon of *Glossanodon musceli*. These fossils have been found at Choczniia at an exposure wherein the uppermost part of the Dynów Marl and the lower part of shales of the Rudawka Tractionite members occur. At Krakowica, a specimen of *Glossanodon musceli* has been found in the Ty-lawa Limestone.

From Wola Radziszowska (Wola R.*), i.a., *Merluccius macroactus* (revision by Jerzmańska, 1968) has been reported. Following osteological analysis of the illustration of this specimen reproduced by Kramberger (1879), Świdnicki (1990 ms) concludes that this specimen is different from other fossil *Merluccidae*, including that from Babice – Połanki 2 (BP₂), described by Jerzmańska (1968) as *Merluccius macroactus*.

The last column (ŁW) illustrates a poor set of taxa found in borehole Łodygowice IG-1 near Żywiec, within the Krosno Formation of the Silesian Unit. Apart from three taxa present in the collection, the table has been supplemented by additional taxa of *Alosa* sp., *Clupea sardinites*, and *Lepidopus* sp., cited by Geroch and Nowak (1980) who quote determination by Jerzmańska and Szymczyk (*pers. comm.*). The occurrence of *Holocentroides moldavicus* in this formation confirms observations made at Sobniów that the Krosno Formation was deposited in the southern, i.e., Silesian and Dukla units at the time when the basin was occupied by the upper bathy-pelagic assemblage.

Concluding remarks

The above review of changes of ichthyofaunal assemblages at a number of studied sections leads to a few important conclusions:

1. All the sections bear groups of taxa which are the permanent components of biocoenosis throughout the formation. Some taxa are absent from single exposures owing to either changes in local life conditions, unfavourable for a given taxon, or – usually – unrepresentative sampling, particularly in case of those taxa which constitute a minor component of biocoenosis. It is usually due to these reasons why

a taxon appears and disappears several times when proceeding up the section.

The second group embraces those taxa which occur either solitary or in a more numerous assemblage at a certain height above the base of the formation. These may appear periodically towards the top of the section, or be confined to a certain section segment. This feature, particularly when repeated in different sections, can point to the genuine first appearance of the taxa in question or to their final disappearance from the entire basin or its part (one should also remember about local differentiation of ichthyofauna). Such appearances and disappearances can result from evolutionary processes, although they usually stem from ecological factors. Such a group of taxa is most useful for ecostratigraphic purposes.

2. Another conclusion resulting from the analysis of individual sections is the appearance at successive exposures, i.e., at defined parts of the section, of rapid and very significant increase of the number of specimens of a given taxon. Sometimes, this increase results from mass occurrence of the taxon within one layer only (e.g., No. 42 at PS₆₋₅), or from a rapid increase in the number of specimens in a few successive layers (e.g., at BH₁). This feature can be interpreted as a result of either rapid reproduction of individual taxa, or rapid appearance and disappearance of the reasons for mass mortality. The latter option appears to be supported by the presence of high number of juvenile individuals within a few taxa simultaneously.

Lateral variability of fish assemblages among exposures within the same lithostratigraphic member

A fully justified comparison can be made among assemblages derived from exposures of the Jasło Limestone chronohorizon (Table 20). Unfortunately, only three sites provide representative samples including a sufficient number of specimens: Sobniów (SO: 342), Łubno-Łazek (ŁŁ₁: 132), and Przysietnica (PS₃₊₂: 70), although at different confidence levels and maximum possible errors. A question arises here of the relationship between the number of all taxa (and genera) and the sample size, namely: SO – 20 (13), ŁŁ₁ – 13 (8), and PS_{3+2+II} – 11 (7). These figures usually result from the appearance of single specimens of different taxa within more numerous assemblages. The taxa (and particularly genera) typical of the upper bathy-pelagic assemblage comprise the main component of individual assemblages at different exposures.

A taxon characteristic of the Jasło Limestone, i.e., *Polyipnus sobniowiensis* occurs at nine sites, including even those exposures wherefrom only one fish specimen has been extracted (for instance at KC and BK₁), but it is absent from several other sites (BG, BN₇, G, JZ_b and KN₁) that include single (e.g., BN₇, BG) or even 33 specimens (KN₁). It should be underlined that even such common taxa, as: *Clupea* sp., *Eomyctophum* cf. *koraense*, *Idrissia* sp., *Africentrum* sp., or *Holocentroides* sp. do not occur in all less numerous assemblages of the Jasło Limestone exposures. A striking feature is the lack of taxa belonging to *Vinciguerria* genus, a typically mesopelagic fish, even in well-sampled

exposures (e.g., SO) of the pelagic Jasło Limestone. These taxa occur at H₁₁₉ only. In this respect, the frequency of occurrence of the index taxon *Polyipnus sobniowiensis* appears to indicate its important, key share in the biocoenosis.

The discussed lateral variability of fish assemblages in some other thin lithostratigraphic members can be analysed in successive tables.

Variability within the Kotów Chert Member is illustrated by a comparison of exposures arranged linearly in cross-sections through individual folds, and proceeding towards the Carpathian margin (Table 21). Four representatively sampled exposures (P₁₋₃₊₆, J_{A-C}, SK, WE lower part) display a nearly comparable assemblage. In the least numerous assemblage (P₁₋₃₊₆), exploited from four closely-spaced exposures of the same outcrop, as well as in a similarly large assemblage from exposure WE lower part, most of the taxa have been determined up to genus level. The number of the latter is, hence, lower than in the most numerous species-bearing assemblages (J_{A-C}, SK). Nevertheless, the lack of *Palaorhynchus* sp. at P₁₋₃₊₆ is evident. The basic set of genera: *Centriscus* sp., *Clupea* sp., *Eomyctophum* sp., *Lepidopus* sp., *Palimphyes* sp., *Scopeloides* sp., and *Vinciguerria* sp. occurs at all four exposures, although not always within other, less numerous, assemblages. The latter are usually dominated by: *Clupea* sp., *Lepidopus* sp., and *Palimphyes* sp.

It should be underlined that the presence of *Glossanodon* sp., typical of the neritic-sublittoral assemblage, within the assemblage coming from exposure at Skopów (SK) can result from sampling of the youngest layers of this exposure, representing the top of the Dynów Marl Member (where this taxon appears exceptionally), or the base of the Rudawka Tractionite Member (where it is common). Such a possibility cannot be excluded, because the fossils had been exploited before stratigraphical studies started, and without geologist's supervision.

Variability within the Dynów Marl Member can be analysed on the basis of assemblages collected at ten exposures, wherefrom in three cases (for exposures of the same outcrop) composite assemblages were formed (cf. Table 21). In two cases, at representative numbers of specimens, i.e., at O₂ and S₁ + S₂, the two assemblages do not differ much. Only at Straszydle, *Scopeloides glarisianus* was determined (*Scopeloides* sp. occurs in both assemblages), and in the topmost marl layers also *Glossanodon* sp., besides *Scopeloides* sp., did appear. Hence, we are confronted here with another transitional zone, wherein coexist taxa considered typical of the two neighbouring zones. Less numerous assemblages lack, of course, some of the taxa; nevertheless relatively common are: *Clupea* sp., *Lepidopus* sp., and *Palimphyes* sp., accompanied by remains of a shark *Cetorhinus* sp.

The generic composition of assemblages of the Kotów Chert and Dynów Marl members (at representatively sampled exposures) is fairly similar, although the second member lacks the important *Centriscus* sp. taxon.

Variability of fish assemblages of the younger portion of the Menilite Formation is shown in Table 22. Within the Dukla Unit, the assemblage of exposure WW is associated with the Tylawa Limestone Horizon (Fig. 4: WW), whereas

in the Silesian Unit fish assemblages of exposures RO₁, R_{1, 4}, and KL (Fig. 4) were collected from layers situated not high (7–33 m) above this horizon; and those of exposures RR₁₋₃ and W – from slightly younger layers (30–90 m higher). As far as the Skole Unit is concerned, fish assemblages were exploited from the Rudawka Tractionite Member (whose lower part includes the Tylawa Limestone Horizon), and at some exposures also from the younger members, i.e., the Futoma Diatomite (BN_{3,4,5}, BE₁, WE upper part) and Borek Nowy Sheet-like Shale (HK₁, BP₁, WE upper part) (Fig. 4). In general, these assemblages originate from layers of comparable age and appear to be ecologically homogeneous.

This table, similarly as the previous one, contains exposures arranged from the internal towards external structures, proceeding towards the Carpathian margin. The first group of exposures (from WW to W) is accompanied by exposure CH from the Western Carpathians (Fig. 4), wherein the upper layers of the Dynów Marl Member and the overlying shale-sandstone complex were sampled. The second group (from T₁ to DG and from L to WE upper part), became separated by a row of exposures (from H_{3,4,5} to BE₁), situated in part within the same structures of the Skole Unit, although in a cross-section shifted towards the NW (cf. Fig. 9).

Representative numbers were obtained at 8 exposures only, in three cases due to combining assemblages derived from neighbouring exposures (RR₁₋₃, R_{1,4}, RB_{1,2,3}).

Table 22 clearly shows that ubiquitous genera are: *Clupea*, *Palaogadus*, and *Serranus* display increased frequency.

It is interesting that *Glossanodon*, common in the analysed assemblages, does not occur in two well-sampled exposures: RR₁₋₃ (95 specimens) and DG (145 specimens). Moreover, *Eophycis* is absent from fairly numerous assemblages of RR₁₋₃, R_{1, 4}, P₄ and RB_{1,2,3}. Ephemeral occurrence of rare taxa, even within relatively large assemblages, is fully understandable and has been referred to before. The lack of species taxa at some exposures, and simultaneous occurrence of respective genera, like, for instance, *Palaogadus simionescui*, *Serranus budensis*, or *Glossanodon musceli* at exposures H_{3,4,5} – BE₁ can be explained by imprecise determination, and not the genuine absence of these species.

A comparison among fish assemblages derived from the two most detailed sampled exposures, i.e., J_{D-G} (644 specimens) and RO₁ (521 specimens) brings unexpected results. The exposure situated farther away from the primary basin margin (RO₁) lacks shallow-water taxa of *Hipposygnathus neriticus*, *Trachinus minutus*, *Trachinus* sp., but includes a solitary *Sygnathus incompletus*, which appears in large numbers at an exposure situated close to this margin (J_{D-G}). One should remember, however, that these taxa occur only in one layer at Jamna Dolna which could have been either overlooked at Rogi, or occurred below or above the sampled part of the section. Hence, the above observation does not lead to a definitive conclusion. Among other differences, one should list the following: the assemblage of J_{D-G} lacks *Capros* taxa, whereas *Capros radobojanus* are numerous at RO₁; and the last exposure lacks *Lepidopus* taxa which are numerous at J_{D-G}.

Concluding remarks

The above analysis of lateral variability of fish assemblages occurring in thin lithostratigraphic members leads to the following conclusions:

1. The analysed type of variability is smaller than the previously discussed vertical variability.
2. The taxa chosen in previous works as index ones display a fairly stable occurrence, appearing at numerous exposures.
3. Frequently observed differences among less numerous assemblages usually stem from unrepresentative sampling, whereas the absence of some taxa within sufficiently representative assemblages may result from the presence of the accepted 10% error.
4. Solitary assemblages bearing numerous specimens lack sometimes common taxa; and display at places a rapid increase in the number of specimens of some taxa like, for instance, *Serranus budensis* at RO₁ or *Glossanodon musceli* at J_{D-G}. These important differences among assemblages whose size guarantees estimation errors not exceeding 5% should be explained by either life conditions or locally occurring events of mass mortality.

However, one more reason should be taken into account. The observed, statistically significant lateral variability can result from a comparison of assemblages derived from the exposures which, in fact, represent different time intervals of a given lithostratigraphic member. This is particularly true when comparing assemblages derived from either thick members, or undivided into members thicker bed sequences of a formation. Such an origin of the observed differences has already been pointed out by the results of statistical studies conducted in the 1970s (Kotlarczyk *et al.*, 1975). An attempt at subdivision of the sections of individual exposures into segments comprising homogeneous fish assemblages (up to the genus level), and further comparison of such segments among the exposures using the Rodionov's technique pointed to the lack of statistical similarity between the neritic-littoral assemblage from Jamna Dolna (J_{D-G}) and analogous assemblages from Równe (R₁₋₃), as well as those from all three homogeneous segments of the Rogi exposure (RO₁). Judging from geological setting of the assemblages in question in respect to the top of the Dynów Marl Member (cf. Fig. 4: Ł-J, R), the assemblage from Jamna Dolna is older than those from Rogi and Równe. The discussed lateral variability within the same ecological assemblage could represent, therefore, an apparent variability reflecting either general or local vertical variability of the assemblage.

The above statistical studies have brought important results when comparing assemblages derived from those exposures that are situated close to each other and are nearly coeval. It has been documented that homogeneous assemblage from Równe does not differ statistically from homogeneous sub-assemblages derived from the upper (layers 1–4) and lower (layers 6–11) portions of the exposure at Rogi (which do not differ among themselves), but it differs significantly from the sub-assemblage derived from the medial layer no. 5, already described in chapter: Variability... among ...layers, from the same exposure. This means that in a small area, within the existing homogeneous assemblage of a given age, one can find episodically and locally occurring such a qualitative-quantitative configuration of taxa which forms a sub-assemblage differing statistically from the entire parent assemblage.

Hence, a methodical conclusion can be drawn that when studying lateral variability among coeval exposures one cannot compare assemblages exploited from one layer with those obtained from a longer section.

The studies conducted with the help of Rodionov's technique gave also another unexpected result. The appearance of one layer (E₁) bearing three additional taxa within homogeneous and relatively long-lasting (layers D₁ to G₃) assemblage from Jamna Dolna was not treated by the applied technique as a break in homogeneity. This finding is compatible with the idea that changes of such type within a fish assemblage do not reflect genuine biocoenose changes (as in the case of the assemblage from layer 5 at Rogi), but results from the activity of post-mortem factors.

A NEW ATTEMPT AT PRECISE ICHTHYOFAUNAL ZONATION

It has been pointed out in previous chapters that ichthyofaunal assemblages tend to reveal rapid changes, observed both at individual exposures and in synthetic and composite sections. Some of these changes are accompanied by either appearance or disappearance of characteristic taxa, acknowledged in previous ecostratigraphic attempts as index taxa for the distinguished zones. Therefore, one could assign such changes to the boundaries of respective zones. Nevertheless, there still remains a number of rapid appearances of smaller or larger assemblages bearing new taxa (and less distinct disappearances of some other assemblages) within previously established zones or within unstudied intervals between the zones. The usefulness of such changes for a more detailed zonation requires consideration. This applies particularly to the boundaries between assemblages derived from exposures: KI and KI_{1+1a} at Krępak; B₁ + B_c and B_a, as well as B_a and B₄ at Błazowa; H₁₊₂₊₇ and HD₃₊₁ at Hłudno; BP₂ and PB at Babice; PS₇ and PS₆₊₅, as well as PS₆₊₅ and PS₃₊₂ at Przysietnica. The existing zonation was established at the time when the sections of the Menilite Formation between zones 3 and 4, 4 and 6, and above zone 6 were not studied in detail.

It should be mentioned in this place that the first subdivision of the Menilite Formation into 6 ichthyofaunal zones (Fig. 10) was mainly based on sections situated in the Skole Unit, close to the town of Bircza. Exposures at Jamna Dolna (J_{AC}, J_{DG}), Krępak IV (KIV₁₋₅), Krępak III (KIII), and Krępak II (mainly: KII₁, KII₂, KII₃, KII) were acknowledged as the stratotypes of successive zones IPM1, 2, 3, 5, and 6. The most distant exposure of the Jasło Limestone at Łubno - Łazek (ŁŁ₁) near Dynów, in turn, was chosen as a stratotype of the IPM4 Zone.

Any successful biostratigraphic subdivision, including ecostratigraphic one, of any formation has a number of requirements, namely:

1. precise location of fauna-bearing exposures in every studied lithostratigraphic section;
2. proper correlation of exposures among the sections;
3. reconstruction of the succession of characteristic faunal assemblages or individual taxa within a complete section;
4. correlation of these assemblages and taxa among the sections of the study area;
5. deciphering the origin of absence of some assemblages from individual sections (lack of exposures, incomplete sampling, tectonic reductions, facies changes, palaeoenvironmental changes).

Age	Strato-type	Ecological assemblage	ZONE		SUBZONE		Other species	
			Representative taxa	Symbol	Representative taxa			
O L I G O C E N E	Kępak	bathypelagic	not investigated				<i>Eomyctophum menneri</i> <i>Eomyctophum koraense</i> <i>Merluccius inferus</i> <i>Hemithysites rumanus</i> <i>Thyrsooides zarathoustrae</i>	
			9. <i>Argyropelecus cosmovicii</i> (A) Alepocephalidae (B) Nessorhamphidae	IPM6	1. <i>Syngnathus incompletus</i>			
	Łubno		8. <i>Polyipnus sobnioviensis</i>	IPM4				
	Kępak	neritic sublittoral	not investigated					
			7. <i>Bregmaceros filamentosus</i> 6. <i>Kotlarczykia bathybia</i> 5. <i>Polyipnus brevis</i>	IPM3				
	Jamna	bathypelagic		4. <i>Paleogadus simionescui</i> 3. <i>Glossanodon musceli</i>	IPM2			
			1. <i>Scopeloides glarisianus</i> 2. <i>Eomyctophum limicola</i>	IPM1	3. <i>Centriscus heinrichi</i> 2. <i>Centriscus teleajensis</i> 1. <i>Centriscus longispinus</i>			
G l o b i g e r i n a m a r l s								

Fig. 10. The first attempt at ichthyofaunal zonation in the Skole Unit of the Polish Carpathians (after Kotlarczyk & Jerzmańska, 1976)

Regarding this study, many years of fieldwork, detailed geological mapping, reconstruction of facies changes of the Menilite and Krosno formations, discovery of different correlative horizons, as well as provisional lithostratigraphic subdivision of the two formations enabled for successful realisation of the first, second, and fifth tasks. More and more detailed, over the years, sampling of successive sections and extension of field studies into the Subsilesian and Boryslav-Pokuttya units, in turn, made it possible to fulfill (although not completely) the third requirement, whereas correlation of the observed changes among assemblages within the lithostratigraphic log contributed to the task number (4) and helped in final ecostratigraphic subdivision.

The collected material enables one to verify previous zonation schemes (see the latest proposal of Kotlarczyk and Jerzmańska, 1988a), regarding both the creation of new zones together with identification of their index taxa, and more precise determination of the boundaries of previously distinguished zones and supplementation of their index taxa inventory.

Verification of the IPM5 Zone, identified in a limited area only, can serve as an example of the applied procedure. This zone was distinguished by Kotlarczyk and Jerzmańska (1976) in its stratotype area, i.e. at Kępak (exposure KIII) and Huta Brzuska (exposure HB₆), within a portion of the Menilite Formation which is comprised between the Jasło Limestone Horizon and Lopyanka Member. The generic composition of fish assemblages collected at these exposures is shown in Fig. 11.

An analogous fish assemblage was found in the same formation at Bachów section (upper part of exposure BH₃), maintaining comparable position in respect to the Jasło Limestone Horizon. This section does not include the entire Lopyanka Member, but only solitary intercalations of calcareous sandstones of the Lopyanka type within the Menilite shales.

Another locality bearing a similar fish assemblage was found in two successive exposures of comparable age at Siemowica (SE₂, SE₃), in the Dobra section (Fig. 9), situated farther to the W. There crops out the Lopyanka Member including numerous intercalations of marly Menilite shales that contain ichthyofauna. The Jasło Limestone Horizon, in turn, was identified in a nearby section of the Menilite Formation on the left bank of the San River (Haczewski, 1989), as well as in more distant sections (e.g. Zawadka), stratigraphically situated between 100 m and 200 m below the fauna-bearing locality.

A similar assemblage was also found farther southwestwards, in the Przysietnica section, at exposure PS₁, situated ca. 10 m above the Jasło Limestone Horizon. Elevation differences of the studied localities versus the Jasło Limestone Horizon result from lithological properties of individual sections. The lower position is confined to shale sequences, the upper one characterizes sandstone-shale complexes. A common feature of the studied sections is the occurrence of intercalations of grey and grey-greenish shales, pointing to periodical oxidization of the sediment.

Figure 11 clearly shows that the assemblage assigned to

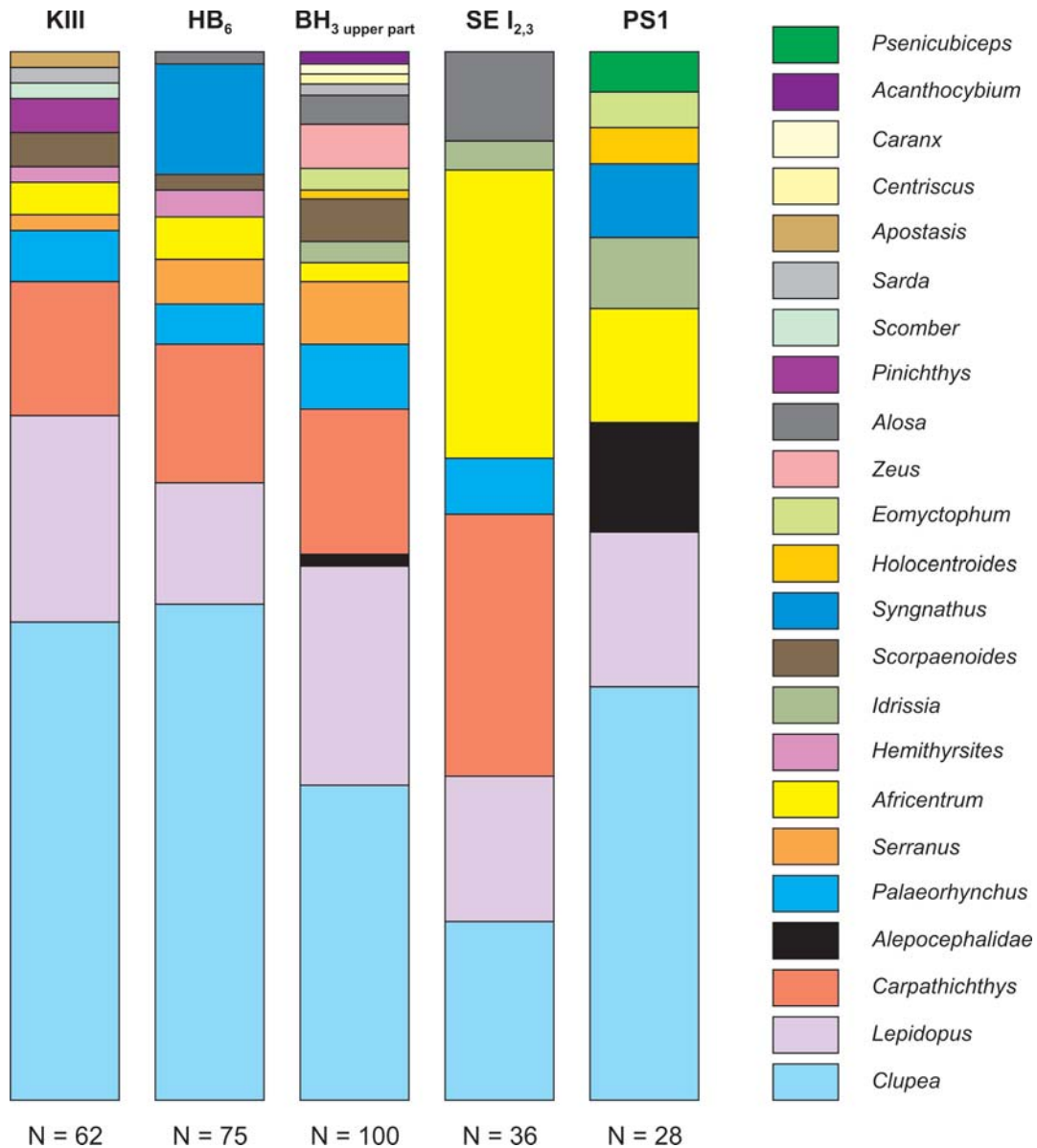


Fig. 11. Generic composition of ichthyofaunal assemblages collected at exposures of zones III (Krępak III, Huta Brzuska 6, Bachów 3 upper part), VI (Siemowica I₂₋₃), and VII (Przysietnica 1), assigned to IPM 5 Zone. Height of column – 100%

the IPM5 Zone is largely composed of taxa occurring in all zones, like: *Clupea* and *Lepidopus*, while some of them are absent from solitary exposures (*Paleorhynchus*, *Serranus*, *Syngnathus*, *Alosa*), and the remaining ones are typical of the upper bathy-pelagic assemblage (*Africentrum*, *Holocentroides*, *Idrissia*, *Scorpaenoides*).

A characteristic taxon, showing a considerable share within the assemblage, is *Carpathichthys*. Although exposure PS₁ contains only identifiable representatives of family (Alepocephalidae), to which this taxon belongs, exposure PSO in the same locality (unidentified, but most probably including also the lower part of bed sequence known from exposure PS₁) does include a well-documented species of *Carpathichthys polonicus*. Therefore, one can safely assume that specimens of Alepocephalidae present at PS₁ represent genus *Carpathichthys*.

Quantitative proportions of all important taxa are similar at every exposure. This fact, apart from the presence of

index taxon, appears to confirm the established correlation among the exposures. On the other hand, it points to a certain stability of the assemblage of Zone IPM5. The question of stability of the IPM1, IPM2, and IPM4 zones has already been discussed in latter chapter.

A new attempt at ichthyofaunal zonation takes into account the necessity of introducing a greater number of zones within the upper bathy-pelagic assemblage, including a section of the Krosno Formation.

In order to maintain the commonly accepted zonal notation, the newly distinguished zones are marked by upper case letters, supplementing the numbers of the existing zones, in such a way that A denotes lower-situated, and B (or – when necessary – succeeding letters) marks the overlying zone(s).

Taking into account the earlier-described changes in ichthyofaunal assemblages, the following zones have been proposed: IPM4A, including a portion of the formation that

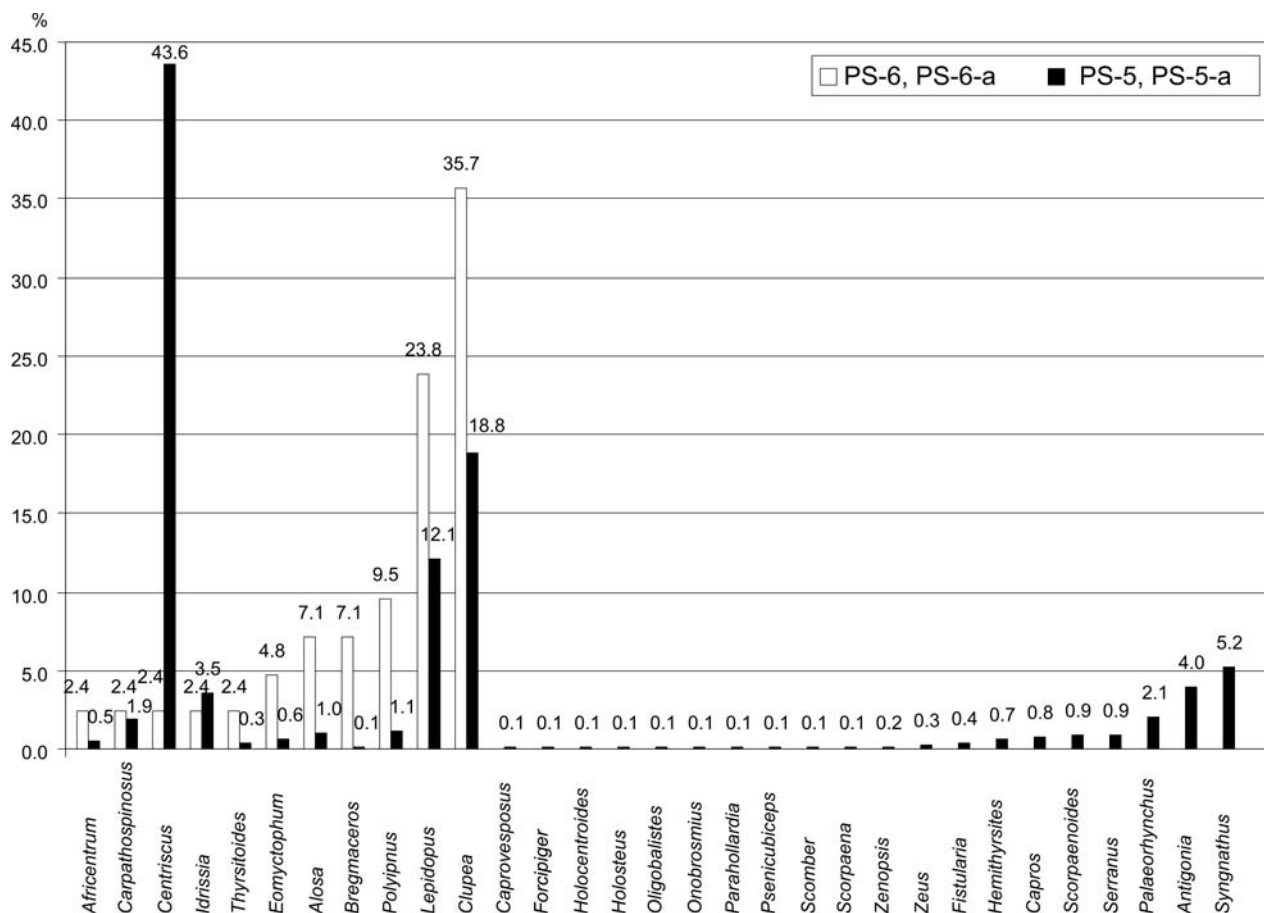


Fig. 12. Percentage of fish genera in exposures PS_{6+6a} and PS_{5+5a} at Przysietnica, representing the newly-proposed IPM 4A Zone

is comprised between the IPM3 Zone and the Jasło Limestone Horizon (represented, i.a. by exposures PS_{4,5,6}); IPM4B, including a segment of the section that is situated immediately above the Jasło Limestone Horizon (represented, i.a. by exposures KI_{1,1a}); IPM6B, including the upper part of the IPM6 Zone where, apart from index taxon *Argyropelecus*, there also appear representatives of family Alepocephalidae (represented by exposures B₄ and PS_{8, 8a, 8b}); IPM6C, embracing the upper part of the Menilite Formation in the Skole Unit where, despite fish abundance, the index taxon *Argyropelecus* has not been found (represented, i.a. by exposures KII, HD_{1,3}); IPM6D, embracing the uppermost part of the Menilite Formation, shortly below the Niebylec Shale Member, and bearing an impoverished ichthyofaunal assemblage (represented, i.a. by exposures PB, BR_{1,2,3}); and INM0A, embracing a segment of the Krosno Formation close to the main tuff horizon (T. V) (represented by an exposure at Harta). A short discussion of these proposals will be given below.

IPM4A Zone

This portion of the Menilite Formation has not been sampled at the Krepak stratotype section, due to the presence of a packet of thick-bedded Kliwa sandstones bearing only thin shale intercalations (Fig. 4). The other sections are either of similar character (e.g. Leszczawa, Hłudno) or are

represented by infrequent exposures bearing fish assemblages typical of the upper bathy-pelagic assemblage, without characteristic taxa (e.g. Łodzinka Ł₂). In a few sections, that portion of the formation either remains obscured (e.g. near Błazowa), or unexploited (e.g. close to Straszydle and Borek Nowy). The only one, exhaustively exploited section at Przysietnica provides abundant fish material whose properties justify distinguishing a new zone. The collected ichthyofauna represents mainly the lower segment of a 35-m-thick interval which is comprised between the upper and lower horizons of laminated limestones (Fig. 4: PS). This segment has already been described in previous chapters: Variability... among ...layers and Variability... among... exposures. Fish specimens have mainly been collected at exposure PS₅ and the uppermost part of exposure PS₆, including Wujskie Limestone Horizon. From the point of view of generic composition (Fig. 12), both qualitative and quantitative differences between these two exposures become apparent: the assemblage of exposure PS₅ is richer in genera, although of negligible share (< 1%) except for genera *Antigonia* and *Syngnathus*; while the assemblage of exposure PS₆ bears a higher amount of some of those taxa which are common in the upper bathy-pelagic assemblage. The most important differences consist in considerable proportion of genus *Bregmaceros* at exposure PS₆, and overwhelming dominance of genus *Centriscus* (occurring mainly in layer no. 42) at exposure PS₅.

The following taxa should be considered characteristic of the newly distinguished zone: 1) a new species (and genus) – *Carpathospinosus propheticus*, discovered and described in this zone (Tyler *et al.*, 1993); 2) a new, not yet described, species *Centriscus* sp. nov.; and 3) genus *Antignonia*, whose climax occurs in this zone. Moreover, a marked feature is the presence of genus *Centriscus* which appears for the second time in the Menilite Formation and for the first time in the upper bathy-pelagic assemblage. A new species, *Syngnathus typus* A, occurs for the first time in the formation, shortly above the lower boundary of the IPM4A Zone.

The above assemblage has no equivalents among any of the studied exposures, including those maintaining a similar position in respect to the Jasło Limestones. The only exception is exposure WZ-6 at Wujskie, also situated in the Sub-silesian Unit, where a layer rich in *Centriscus* has been found in between layers of laminated Wujskie Limestones. This layer is an equivalent of layer no. 42 at Przysietnica.

IPM4B Zone

At the stratotype Krępak section, a ca. 7-m-thick segment of the Menilite Formation (KI_{1,1a}), starting ca. 8 m above the Jasło Limestone Horizon, has been sufficiently sampled. The fish assemblage is composed of taxa common for the upper bathy-pelagic assemblage: *Africentrum* sp., *Alosa* cf. *sagorensis*, *Alosa* sp., *Apostasis* sp., *Echeneis carpathica*, *Eomyctophum* cf. *koraense*, *Holocentroides moldavicus*, *Holocentroides* sp., *Idrissia* sp., *Merluccius* sp., *Palaeorynchus* sp., *Polyipnus anteasteroides*, *Thyrstitoides* sp., *Zeus faber*, as well as of even more common taxa, already known from the lower bathy-pelagic assemblage (cf. Table 11). A portion of the Menilite Formation exposed in the lower part of Bachów-3 (BH_{3bp}) exposure (Fig. 4: BR; Fig. 6) attains a similar stratigraphic position, i.e. 15 to 20 m above the Jasło Limestone Horizon. Its fish assemblage is comparable, and – taking into account those taxa whose share exceeds 1 per cent – even identical to that of Krępak (cf. Fig. 13). The dominant taxa are, however, different, being represented by *Holocentroides* (42.8%) and *Africentrum* (11.7%) at Bachów, and by *Eomyctophum* (18.2%) at Krępak. Only one layer at Bachów (A₁; Table 8) does contain an unexpectedly appearing taxon characteristic of the IPM6 Zone, i.e., one specimen of *Argyropelecus*. This appearance should be treated, as already commented upon in chapter: Variability... among ...layers, as F_EAD (first ecological appearance datum), and not as an indicator of the IPM6 Zone.

It should be mentioned in this place that the studied fish collection includes one specimen of *Kotlarczykia* sp., found in a heap of one of exposures at Bachów. The attached archival label implies that A. Jerzmańska must have had doubts as to the location of this specimen. Hence, it cannot be excluded that this specimen could have been found at an unexploited exposure situated farther upstream of exposure BH₃, where layers of the Jasło Limestone Horizon and older ones, i.e., representing the IPM3 Zone, do crop out. In such a case, the position of the discussed taxon would be compatible with the zonal scheme. An alternative explanation is

that a specimen of *Kotlarczykia* could have been found at one of exploited exposures like, for instance, BH₃. Therefore, its appearance in the basin should be treated as L_EAD (last ecological appearance datum), and not as a zonal marker. If the last mentioned location of *Kotlarczykia* specimens were correct, an unprecedented in the Polish Carpathians coincidence of this taxon with that of *Argyropelecus* would occur. Such a coincidence has been reported by Gregorová (1997) from the Šitbořice Member in the Cieszyn Silesia region.

The other exposures showing the layer sequences of similar stratigraphic position in respect to the Jasło Limestone Horizon, namely: T₂ at Temeszów, and MR₂ and MR₃ at Mrzygód (Table 14), provided insignificant number (7) of specimens, representing four common generic taxa.

It is likely that the sequence of layers at an unidentified exposure PSO at Przysietnica included, judging from the sampled rock material and assemblage composition, the Jasło Limestone Horizon, the base of the IPM5 Zone (one specimen of *Carpathichthys polonicus*), and an intervening packet of layers equivalent to those at exposures KI₁ and BH₃lower part. The fish assemblage (cf. Fig. 13), dominated – similarly as at KI₁ – by *Eomyctophum* (42.5%), includes (although not every one and showing different proportions) common taxa known from exposures KI₁ at Krępak and BH_{3bp} at Bachów. Similarly to the latter exposure, exposure PSO bears *Syngnathus*, typus A and one specimen of *Argyropelecus*. If the inferred stratigraphic position of exposure PSO (cf. Fig. 4: PS) is correct, we are confronted here with another example of an early, signal appearance of *Argyropelecus* shortly above the Jasło Limestone Horizon.

The differences between fish assemblages of the proposed new IPM4B Zone and those of IPM4 Zone (cf. Table 23) consist in the lack in the former zone of species *Polyipnus sobniowiensis* and very rare taxa, like: *Equula* (?) sp., *Oligolactoria bubiki*, *Alopecias* sp., as well as *Hemithyrsites* sp., which is common in the upper bathy-pelagic assemblage and rare in the IPM4 Zone. The lack of rare taxa can be a result of sampling error. On the other hand, the IPM4B Zone lacks such species taxa, like: *Eomyctophum menneri*, *Idrissia carpathica*, *Priacanthus longispinus*, *Vinciguerrria merklini*, and *Vinciguerrria obscura*, although their generic counterparts are present. This suggests that the studied specimens are devoid of diagnostic features.

On the other hand, the postulated IPM4B assemblage includes those taxa which are absent from the IPM4 Zone, namely: *Alosa* cf. *sagorensis*, *Alosa* sp., *Apostasis* sp., *Cetorhinus* sp., *Echeneis carpathica*, *Nessoramphus* sp., *Palaeogadus distinctus*, *Palaeomolva monstrata*, *Scomber voitestii*, *Scorpaenoides* sp., *Serranus* sp., *Syngnathus incompletus*, *Syngnathus* sp. – typus A, *Syngnathus* sp., and *Thyrstitoides* sp. Some of them appear in the basin already below the IPM4 Zone, whereas others pass into the zones situated above the IPM4B. In other words, the proposed zone does not contain representative taxa; the assemblage is composed of taxa typical of the upper bathy-pelagic assemblage. Hence, there is hardly any ground to distinguish a new zone. In this case, it has been decided to assign uncharacteristic fish assemblages derived from exposures situated immediately above the Jasło Limestone Horizon to either

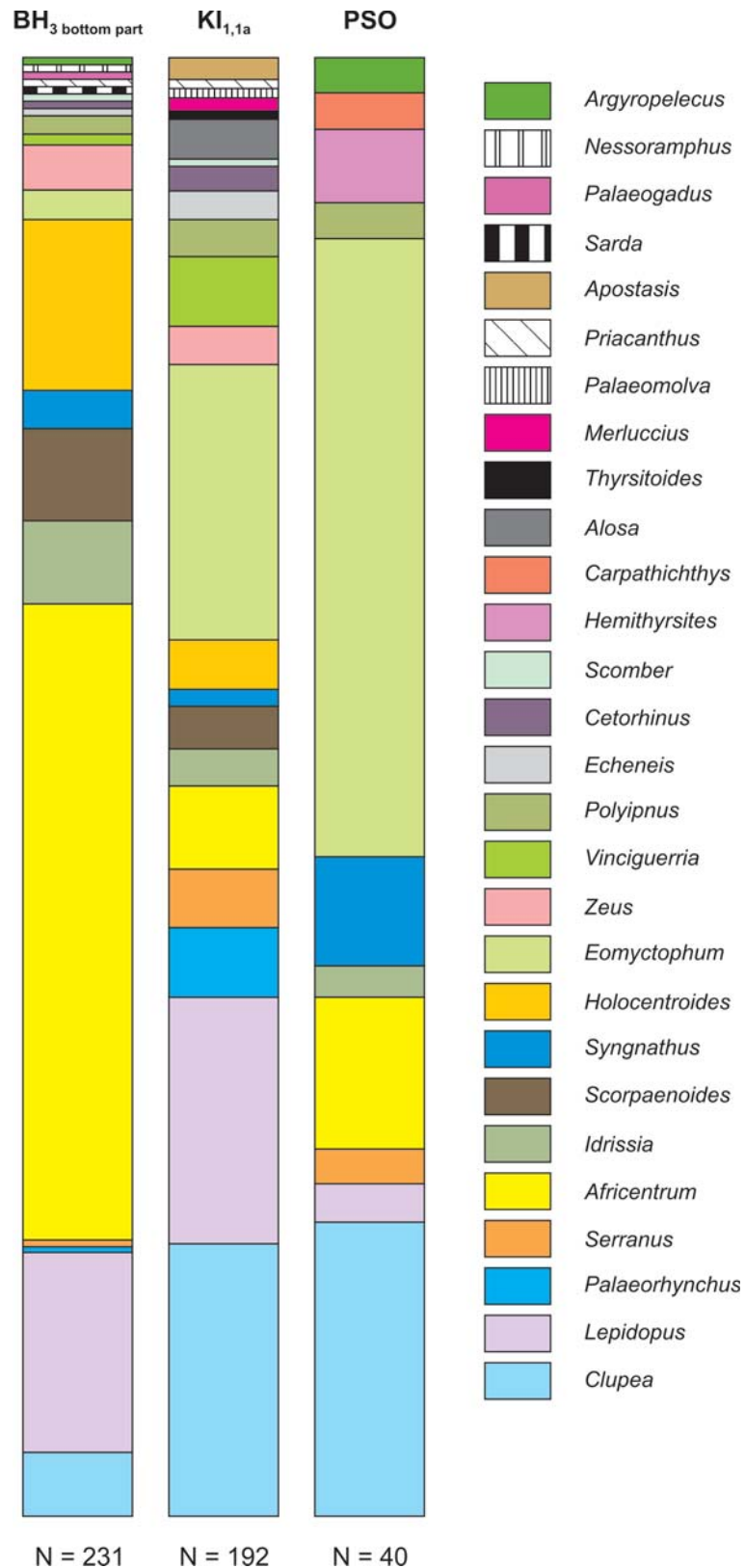


Fig. 13. Generic composition of ichthyofaunal assemblages collected at exposures of zones III (Kępak 1+1a and Bachów 3 bottom part) and VII (Przysietnica O), and treated as representatives of the newly-proposed IPM 4B Zone

IPM4 (KI_{1,1a}, MR_{2,3}, T₂), or IPM5 (BH₃) zones, or – taking into account insufficient data – to the upper bathy-pelagic assemblage (PSO) only.

Table 23 compares the share of taxa present at exposures of the Jasło Limestone Horizon (IPM4) to that identified at exposures situated below this horizon (IPM4A Zone), and at exposure KI_{1,1a} which is situated above (IPM4B Zone). This comparison illustrates very well both the necessity of distinguishing IPM4A Zone and, at the same time, redundancy of the IPM4B Zone.

IPM6B Zone

The idea of separating an additional IPM6B Zone from the existing IPM6 Zone originated from an analysis of fish assemblages collected at exposures B₄ (Table 12) and PS₈ (Table 17). These assemblages contain infrequent Alepocephalidae, besides taxa characteristic of both the IPM6 Zone and upper bathy-pelagic assemblage. It should be mentioned in this place that none of those exposures which represent the underlying portion of the Menilite Formation and bear the fish assemblage characteristic of the IPM6 Zone does contain representatives of this family. In some cases, fish assemblages collected at these exposures are very large (BH₁ – 1,291, KII₃ – 575, BP₂ – 207, B₁ – 126 specimens), limiting a possibility of non-finding during exploitation. This fact appears to indicate re-appearance of Alepocephalidae in the basin, although partially in new area (IV).

The only one characteristic taxon of this zone is represented by one specimen of *Propteridium* sp., found at exposure B₄. This fact hardly justifies identification of a new zone IPM6B, therefore, assemblages bearing slickheads have been assigned to the IPM6 Zone.

IPM6C and IPM6D Zones

A careful study of the upper part of the Menilite Formation at numerous exposures aligned (cf. Fig. 4) on the sections of Błazowa (B₂, B₃, B₅, B₆, B₁₅, B_k; Table 12), Brzuska (BR₁, BR₂; Table 11), Hłudno (HD₁, HD₃; Table 13), and Krępak (KII; Table 11), as well as at solitary exposures of Kąkolówka (KK₂; Table 12), Krzemyk-Dynów (KD; Table 12), Przedmieście Babickie (PB; Table 15), and others (DU₁; Table 16, KS₁; Table 14, PP) leads to a conclusion that the index taxon of the IPM6 Zone – *Argyropelecus cosmovicii* could have not survived until the final episodes of deposition of this sequence in the Carpathian basin. Reliability of this statement can be enhanced in a few cases by the large size of exploited fish assemblages (HD₁ – 217, HD₃ – 36, KII – 98, KK₂ – 42 specimens).

Therefore, there are good reasons to distinguish one or even two (IPM6C and IPM6D) ichthyofaunal zones younger than that of IPM6, within a few tens of metres thick portion of the formation. The studied exposures enable one to trace the lithostratigraphic boundary between the Menilite and Krosno (Niebylec Member) formations, providing a good opportunity for a comparison between the assemblages derived from younger and older strata.

A study of fish assemblages of the above exposures indicates that nearly 30 taxa do not pass over the IPM6 Zone

in the Carpathian basin (see also Table 25). These taxa are usually represented by infrequent specimens, therefore, their absence can be a result of insufficient sample size. Nevertheless, one should take notice of the fact of simultaneous absence of previously more numerous taxa, like: *Zeus faber* sp., *Zeus* sp., *Antigonia* sp., *Capros radobojanus*, *Polyipnus* sp., and *Polyipnus* cf. *anteasteroides*. One should also add that all exposures of that part of the Menilite Formation are devoid of specimens of families Zeidae, Caproidae, and Sternoptychidae, to which the above genera belong.

The fish assemblage collected from exposures (PB; BR₁₂; DU₁; KS₁; PP) of the above-proposed IPM6D Zone is even more impoverished than that of the lower-situated IPM6C Zone. Thirteen taxa of the latter zone, as well as taxon *Vinciguerrria* sp. do not pass into the IPM6D Zone. Nevertheless, the preservation of *V. distincta* species in the IPM6D Zone enables one to neglect this absence. On the other hand, most of the above-mentioned 13 taxa are very poorly marked in the IPM6C Zone, being represented by one specimen only. More numerous are: *Idrissia* sp. (15 specimens), *Africentrum* sp. (3 specimens), *Fistularia* sp. (3 specimens), *Holocentroides moldavicus* (3 specimens), *Serranus* sp. (3 specimens) and *Echeneis carpathica* (2 specimens). Taking into account the small number of specimens within samples collected at exposures of the zone in question (the most numerous one of which, i.e. PB, providing only 25 specimens), the absence of some taxa can be explained by high sampling error, while the disappearance of more numerous taxa, like: *Idrissia* sp. and Sternoptychidae (typus-xz) appears to indicate a gradual, time-prograding elimination of meso-bathypelagic fish taxa from the Carpathian basin, until their complete disappearance in the Early Miocene.

The occurrence of characteristic short-lived taxa is crucial to ecostratigraphy. In this case, the postulated IPM6C Zone bears only one such taxon, i.e. of a shark *Notidamus* (1 tooth), while Zone IPM6D is devoid of such taxa at all.

An analysis of fish assemblages leads to a conclusion that, at the present state of recognition, there are no sufficient data to distinguish two separate zones: IPM6C and IPM6D, although the boundary between the two combined assemblages of these zones and that of IPM6 Zone is fairly well documented. This boundary is characterised by disappearance of an index taxon *Argyropelecus cosmovicii* and other characteristic taxa of the IPM6 Zone (*Paraberyx bachoviensis*, *Paraberyx* sp., *Capros medianus*, *Prohollardia avita*, *Protomyctophum* sp., *Archaeus* sp.), alongside with numerous, although secondary taxa which have been dealt with at the beginning. Therefore, a new IPM7 Zone has been distinguished, including the two postulated zones IPM6C and IPM6D.

Zones INM0 and INM0A

In the uppermost part of the Skole Unit sequence, namely in the Leszczawka Diatomite Horizon which is lithologically similar to the Menilite shales, one zone (INM0; Jerzmańska & Kotlarczyk, 1981) bearing an index taxon of *Caranx gracilis* has been distinguished up to now.

This zone will not be numbered until complete description of the fish assemblage from Harta (HT), found in a lower stratigraphic position, is finished.

The INM0 assemblage includes fish specimens collected at Huta Poręby (HP – 26 specimens) and Zahuty (ZH – 10 specimens). Apart from such common taxa, like: *Clupea* sp., *Merluccius* sp., and *Syngnathus* sp., this poor assemblage (Table 13) contains also Early Miocene species: *Caranx gracilis* Kramberger and *Merluccius errans* (Smirnov).

The assemblage of Harta (171 specimens), belonging to the postulated INM0A Zone, includes all the taxa of the above-described assemblage, as well as a few taxa known from previous zones, like: *Alosa* sp., *Lepidopus* sp., and *Leiognathus* sp., and three taxa new to the Carpathian basin: *Merluccius hartensis* Świdnicki, *Leiognathus* cf. *minutus* Daniltschenko, and *Gobius* sp.

The obtained results lead to a conclusion that it is not necessary (although possible) to distinguish a new zone INM0A. The small number of well-studied localities of the two potential Miocene zones and the scarcity of their assemblages require great caution. Therefore, it has been decided to distinguish only one zone of Miocene age, labelled as INM1.

Finally, it has to be marked that in case of precise, future documentation of an Early Miocene age of the entire sequence of layers, assigned to the newly-distinguished IPM7 Zone, a revision of zone numbering will be necessary. The IPM7 Zone will then become the first Miocene zone, INM1, while the present INM1 Zone will be renamed as INM2.

A SEQUENCE OF ICHTHYOFAUNAL ASSEMBLAGES IN THE MENILITE-KROSNO SERIES OF THE POLISH CARPATHIANS

An analysis of the variability of fish assemblages in the stratigraphic log has enabled for a construction of a modified standard ichthyofaunal zonation in the Palaeogene and Neogene of the Polish Carpathians. This standard includes now 9 zones: IPM: 1, 2, 3, 4A, 4, 5, 6, 7, and INM1.

In order to reconstruct the most detailed quantitative composition of the assemblages associated with each zone, individual ichthyofauna-bearing exposures have been classified into respective zones (Table 24), using the methodology described in the previous chapter. The core of every assemblage in each zone is composed of fish collected at stratigraphically important exposures, usually bearing numerous specimens, comprising representative taxa (except for zone IPM7), as well as other characteristic taxa. These exposures are marked in the table by appropriate acronyms. Such groups of exposures have been supplemented by those exposures which bear infrequent specimens, although including index taxa, and even by exposures devoid of such taxa but showing precisely determined stratigraphic position.

The next step consisted in the determination of zonal assemblages and construction of a synthetic diagram portraying ichthyofaunal changes in the Palaeogene and Neogene of the studied segment of the Carpathians (Table 25).

Table 24

Basic and supplementary exposures classified into the distinguished ichthyofaunal zones.

Zone	Basic exposures	Supplementary exposures
INM-1	HP, HT, ZH	
IPM-7	B ₂ , B ₃ , B ₅ , B ₆ , B ₁₅ , B _k , BR ₁ , BR ₂ , DU ₁ , HD₁ , HD ₂ , HD₃ , KD, KII , KK ₂ , KS ₁ , PB , PP	
IPM-6	B ₁ , B _a , B _c , B₄ , BH₁ , BH ₂ , BP₂ , BR ₄ , BR ₅ , BR ₆ , H ₁ , H ₂ , H ₇ , KII ₁ , KII ₂ , KII₃ , KS ₃ , MR ₄ , PS₈ , PS_{8a} , PS_{8b} , PS ₁₀	B _s , BR ₁₀ , KII _b , KII _c , KII _e , KII _h
IPM-5	BH₃ , BR ₁₁ , BR ₃₄ , HB₆ , KIII , PS ₁ , SEI₂ , SEI₃ , T ₃	SEII
IPM-4	BN ₇ , BG, DU ₃ , H ₁₁₉ , KI , KI₁ , KI_{1a} , KC ₁ , KN₁ , LL₁ , MR ₁ , MR ₂ , MR ₃ , PS₂ , PS₃ , PS_{3a} , PSII , SO , T ₂ , T ₄	BK ₁ , JZ _b , Ł ₁ , Ł _{1a} , G
IPM-4A	DU ₄ , KN ₄ , PS ₄ , PS₅ , PS_{5a} , PS₆ , PS_{6a} , WZ ₆	Ł ₂ , WZ _j
IPM-3	KIV₄₋₅ , L₁ , PS₇ , PS _{7a}	
IPM-2	B _m , BB ₁₀₄ , BB ₁₁₈ , BE ₁ , BN ₃ , BN ₄ , BN ₅ , BN _{IX-11} , BP ₁ , BR ₄₃ , BR ₄₅ , BZ, CH, D₁ , D _a , DG , H ₃ , H ₄ , H ₅ , HD _{DS} , HE, HK ₁ , JDG , KI _G , KIV ₁₋₃ , KL, KR, KT _{E-F} , KW, L , M _{2-up} , P₄ , R₁ , RB_{1bp} , RB₂ , RB₃ , RO₁ , RR ₁₋₃ , S _{1b} , S ₃ , SR, ST, T ₁ , W, WE_{up} , WW	J ₃ , J ₄ , R _{4up} , RR ₀₃ , L _s
IPM-1	BO, BR ₂₂ , BR _{22a} , BW, C, F, H ₁₃₂ , H ₆ , HB ₁ , HK ₂ , J_{A-C} , KI ₃ , KC ₂ , KK ₁ , KR ₀ , KT _{B-D} , LA, LL ₂ , M ₁ , M _{2bp} , O₂ , P₁ , P₂ , P₃ , P₆ , PT, RO ₂ , RR ₄ , RR _{4a} , RR _{4b} , S₁ , S_{1a} , S₂ , SK, U, WE_{bp}	BK ₂ , J ₁ , J ₂ , JZ _a , J _{pp} , N, O ₁ , R _{4bp} , RT
IPM-3-7	BE ₂ , BR ₃₉ , HB ₂ , HB ₃ , HDK ₁ , L ₄ , LH ₁ , LH ₂ , LW, ND, PŁ, PS ₉ , PSO, S ₄ , WE _O , WJ ₁ , WZ, WZ ₉	BR ₁₉ , BR ₂₁ , DU ₂ , HB ₅ , HB ₈ , KIV _{2a} , L ₇ , L ₁₀ , NS, RB _{1up} , RB ₄ , WJ ₂ , WZ ₃ , WZ _z

Acronyms in bold mark those exposures which are most important for ecostratigraphic purposes. The base of the table includes exposures assigned to the upper bathy-pelagic assemblage only, without zone indication

The established groups do not include those exposures which have not been identified in the field, although having been known to A. Jerzmańska (e.g. J₁, J₂, B_s, L_s) and J. Świdnicki (e.g. BK_{1,2}, WJ_{1,2}), neither infrequent, less important exposures bearing small number of specimens (e.g. RR₀₃, KII_b), although of well-determined stratigraphic position. Such exposures have been classified into a group of supplementary exposures (Table 24), and fish specimens identified at the latter have been taken into account in a description of the composition of the entire collection (chapter: Composition of ichthyofauna...), and referred to in tables showing lateral variability of zonal assemblages (see the following chapter: Ecostratigraphy ...).

An analogous subdivision into two groups has been applied to those exposures which represent the upper bathy-pelagic assemblage, i.e. devoid of index taxa of the zones IPM3 through IPM7.

As a result, from a collection numbering 12,752 fish specimens (including 10,705 classified into genera and species), 12,289 specimens (including 10,363 classified into genera and species) have been used for further analysis. From the remaining 463 specimens (342 genera and species), 232 (169 genera and species) have been assigned to the upper bathy-pelagic assemblage.

The summarizing Table 25 has been constructed in the same way as tables illustrating synthetic sections. The taxa falling into respective taxonomic categories have been arranged according to their shrinking temporal extent, starting from the first zone. In this way, the last taxa of every zone are its representative taxa, i.e. those which do not occur elsewhere.

The description presented below is based on highly variable numbers of specimens. Zones 1, 2, 4A, and 6 bear more than 1,000 specimens; zones 3, 4, 5, and 7 include between 450 and 1,000 specimens, whereas the youngest zone lists only ca. 150 specimens.

Except for the last case, these are considerable numbers which allow for reliable characteristics of quantitative composition of each zone. For obvious reasons, such a characteristic is based on species-generic composition, and special attention is given to both the representative taxa and those numbering more than 20 specimens.

Many of those taxa which are described below have already been illustrated in previous publications (Jerzmańska, 1960, 1967a, 1968, 1974, 1979; Jerzmańska & Kotlarczyk, 1968, 1975; Świdnicki 1986, 1988a, 1988b; Tyler *et al.*, 1993; Jerzmańska *et al.*, 2001), but equally numerous ones have only been casually mentioned and listed in summarizing compilations. Some of the taxa comprised in the studied collection are described for the first time in this paper. Taking into account monographic character of the latter, it was decided to supplement photographic documentation of the collection, particularly by those forms which had not been published, although taxonomically described. Six figures illustrate: some index taxa of the distinguished zones (Fig. 14); rare taxa, which are characteristic for the zones and may become index ones in the future (Fig. 15); rare taxa which are characteristic for neighbouring zones or different zones of the upper bathy-pelagic assemblage (UBA; Fig. 16); taxa belonging to UBA (Figs 17, 18); as well as taxa

provisionally typified by A. Jerzmańska as types (Fig. 19). The last figure also shows photographs of fish scales, teeth, and filtrative processes of sharks.

IPM1 Zone

This zone includes, in the entire studied area, 37 taxa belonging to the first two taxonomic categories. The number of representative taxa amounts to 11, from the most numerous, like: *Eomyctophum limicola*, *Scopeloides* sp., *S. glarisianus*, *Centriscus heinrichi*, *C. longispinus*, *C. teleajensis*, through infrequent *Vinciguerria talgiensis*, up to solitary ones: *Barbus* sp., *Diaphus* sp., *Palimphytes lanceolata*, and *Scorpaenoides popovicii*.

The generic taxa of the last two species are quite frequently represented in the assemblage, as are: *Centriscus* sp., *Cetorhinus* sp., *Eomyctophum* sp., *Clupea* sp., *C. sardinites*, *Lepidopus* sp., *L. glarisianus*, *Paleorhynchus* sp., and *Vinciguerria* sp. All of them pass into different, higher-situated zones.

A single appearance of *Thyrstitoides* sp. (F_{EAD}), hitherto-found in the upper bathy-pelagic assemblage only, is to be noted, alongside with fairly numerous presence of *Glossanodon* sp., although exclusively in the uppermost part of the zone and at two closely-spaced exposures (S₁/S₂) situated in the axial part of the basin.

IPM2 Zone

This zone lists 41 taxa, including 11 (10?) representative ones. The latter are dominated by: *Glossanodon musceli*, *Trachinus minutus*, and *Hipposyngnathus neriticus*. The last two taxa appear frequently in one layer at Jamna Dolna JDG only. This group includes as well *Palaeogadus simionescui*. Although one specimen of this species has been found at Przysietnica PS_{7A} exposure at its contact with exposure PS₇, comprising the IPM3 Zone assemblage, inclusion into the latter of the fish assemblage derived from exposure PS_{7A} (bearing as well *Serranus* sp. and *Antigonia* sp.) is one of possible options. Even though this option holds true, one cannot neglect the fact that *Palaeogadus simionescui* is a characteristic taxon of the IPM2 Zone.

The less frequently occurring representative taxa include: *Eophycis jammensis*, *Eophycis* sp., *Trachinus* sp., *Hemiramphus jerzyi*, *Pomolobus* sp., *Palaeogadus abbreviatus* and *Holosteus mariae*.

The dominant taxa of this zone include: those which appeared earlier, like *Glossanodon* sp., those present in younger zones: *Serranus budensis*, *Holosteus* sp., and *Ammodytes* sp., as well as those which both pre- and postdated the IPM2 Zone, like: *Clupea* sp., *Clupea sardinites*, *Lepidopus* sp., *Lepidopus glarisianus*, *Serranus* sp., *Palaeogadus* sp., and *Capros radobojanus*. To the less frequently represented taxa belong: *Palimphytes* sp., which survived from the IPM1 Zone, and those which occur in younger zones, like, for instance, *Merluccius* sp., *Syngnathus incompletus*, *Fistularia* sp., *Propercarina* sp., *Palaeomolva* sp., *Pinichthys* sp., *Properca sabbai*, and *Sarda* sp., as well as more long-lived ones, like, e.g. *Caranx petrodavae* or *Scomber voitestii*.

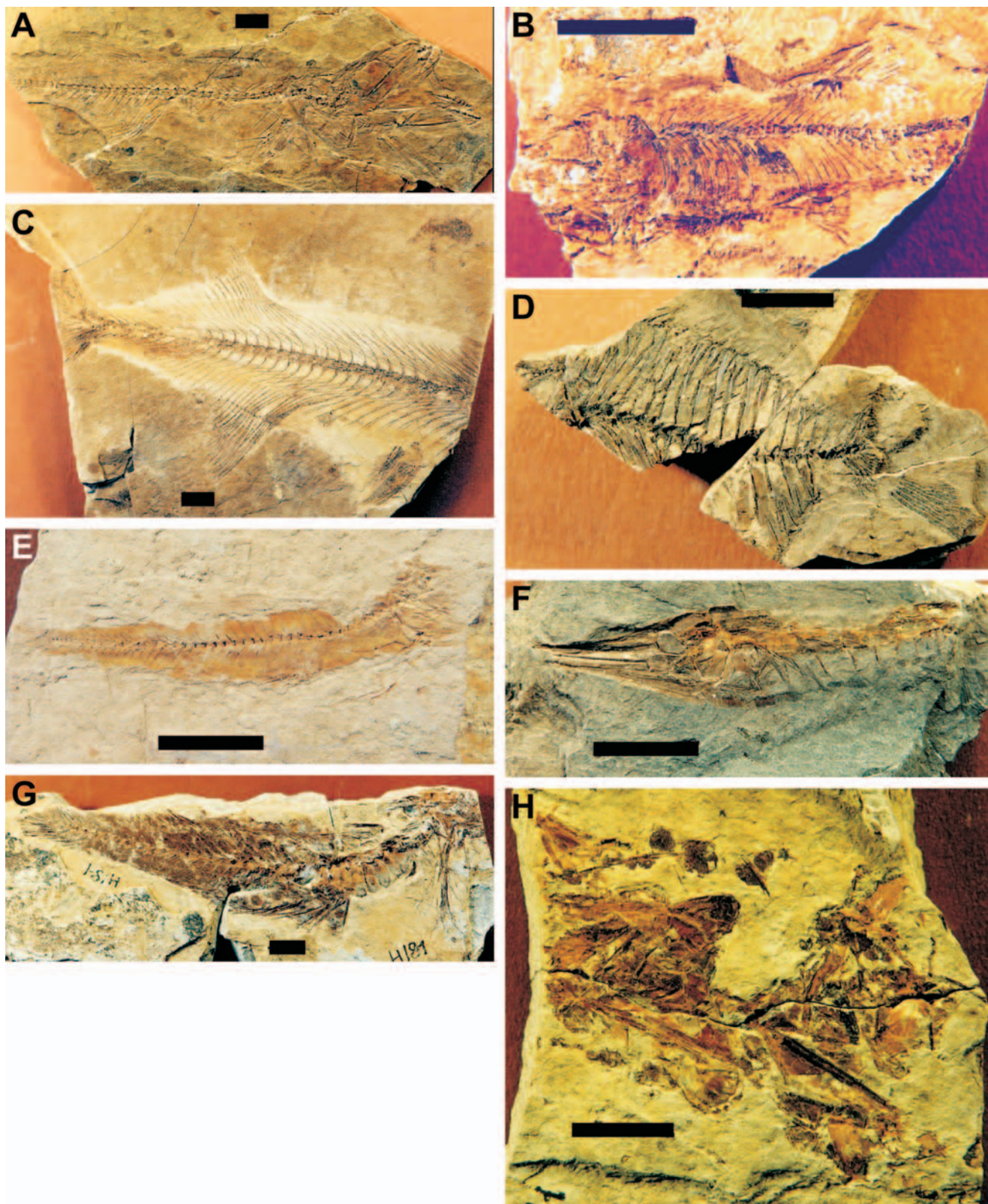
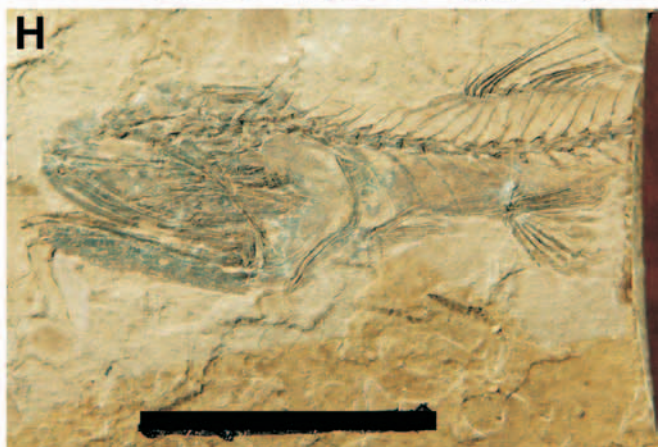
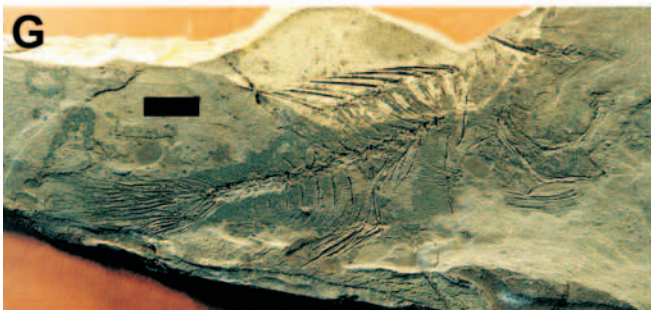
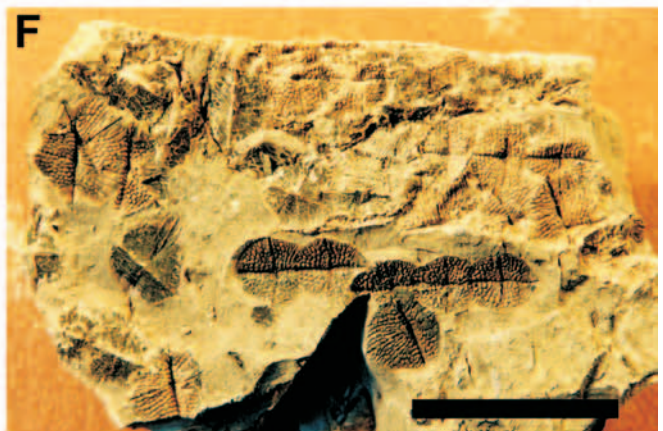
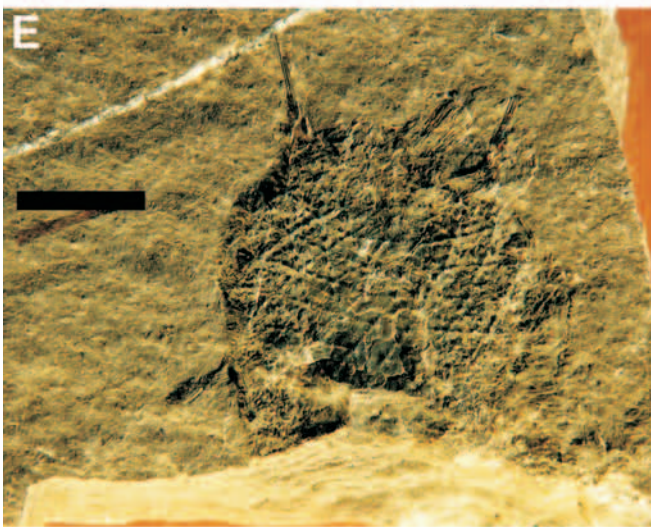
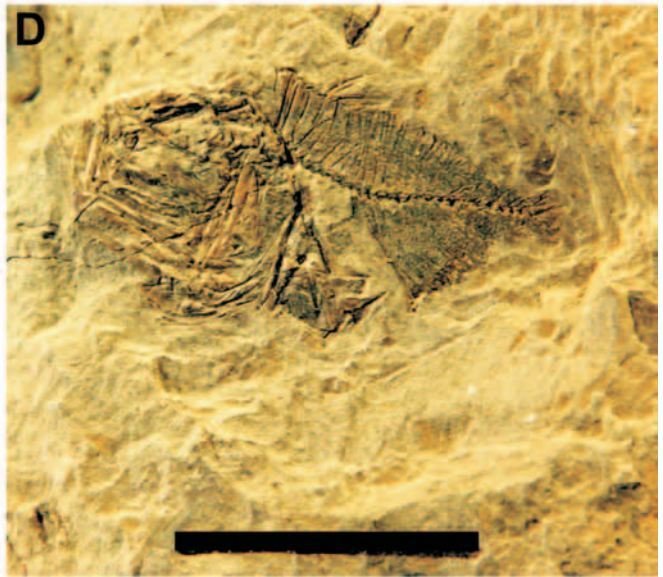
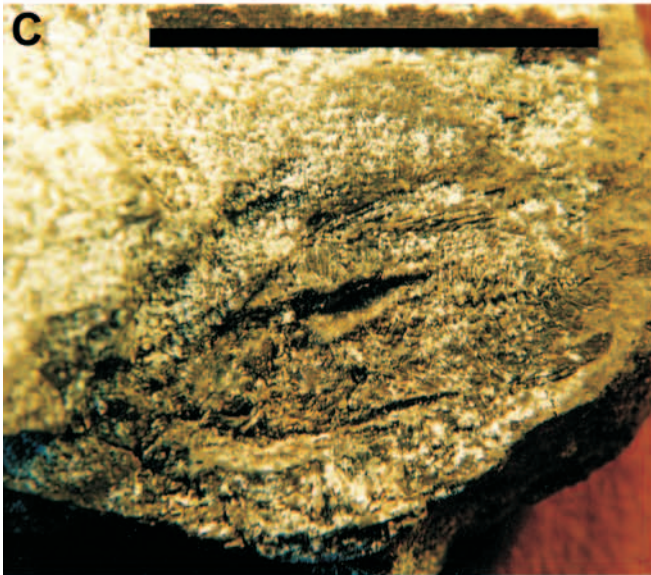
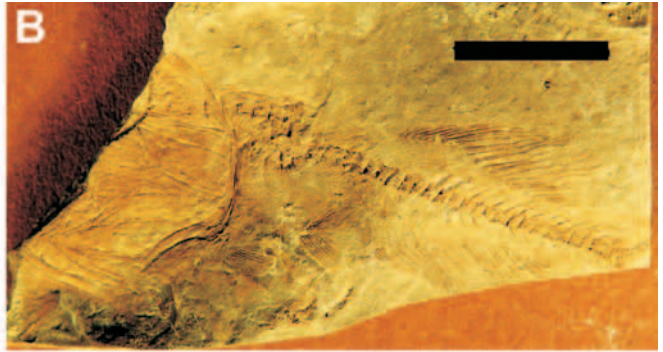
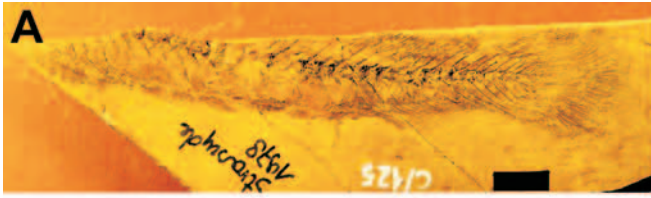
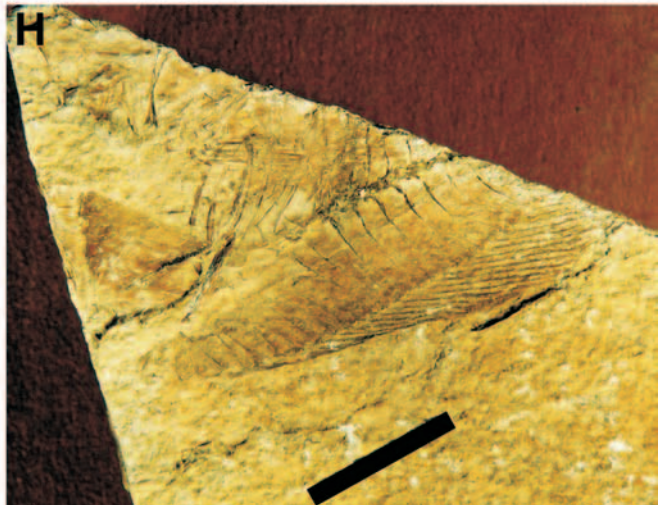
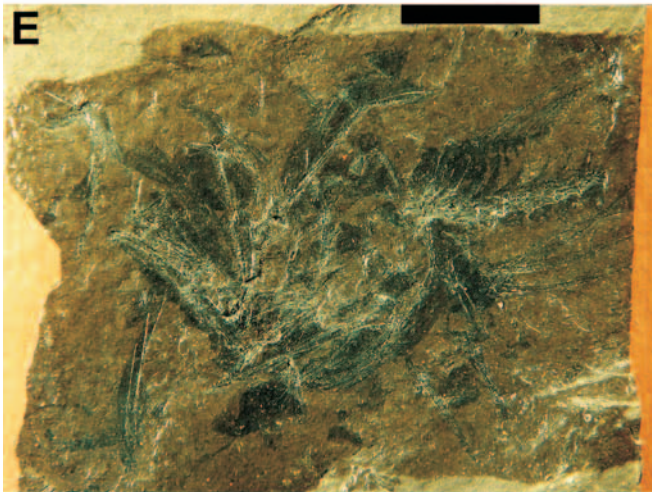
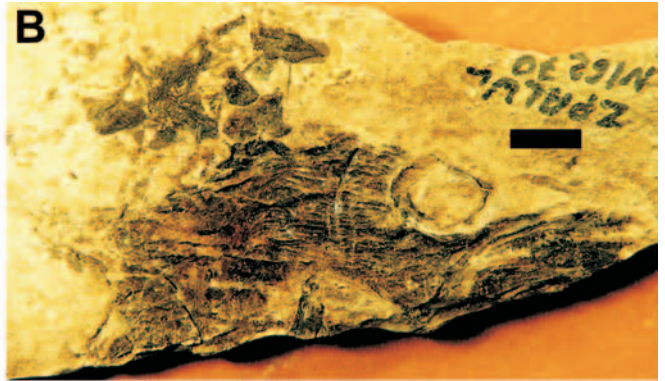
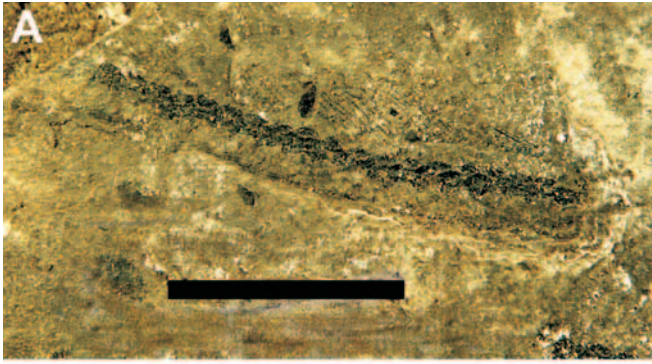


Fig. 14. Zonal index taxa, not illustrated in previous works: **A** – *Palimphytes lanceolata* and **B** – *Vinciguerria talgiensis* (Zone IPM 1); **C** – *Holosteus mariae* (Zone IPM 2); **D** – (*Polyipnus* =) *Horbatschia brevis* and **E** – *Bregmaceros filamentosus* (Zone IPM 3); **F** – *Centricus* sp. nov. (Zone IPM 4A), **G** – *Merluccius hartensis* and **H** – *M. errans* (Zone INM 1)

Fig. 15. Taxa characteristic for some ichthyozones, not illustrated previously. Due to their rare occurrence (1–4 specimens), it is difficult to decide whether these taxa are associated exclusively with the zones listed below: **A** – the oldest representative of Gadiformes, unidentified (Zone IPM 1); **B** – *Bathyprion* sp. (Zone IPM 3); **C** – *Forcypiger* sp. and **D** – *Oligobalistes* sp. (Zone IPM 4A); **E** – *Oligolactoria bubiki* (Zone IPM 4); **F** – *Syngnathus* sp., *typus B* (Zone IPM 5); **G** – *Paraberyx bachoviensis* and **H** – *Protomyctophum* sp. (Zone IPM 6)





It is worth noting that 11 taxa, including 8 deep-water ones, disappear from the basin during the IPM2 Zone time interval.

IPM3 Zone

The IPM3 Zone bears 38 (36?) taxa, including 6 (5?) representative ones. The presence of *Palaeogadus simi-onescui* and *Antigonia* sp. is not certain, since these taxa could be derived from a layer of the IPM2 Zone (see above). Dominating are: *Polyipnus brevis*, *Kotlarczykia bathybia*, *Kotlarczykia* sp., as well as *Bregmaceros filamentosus* and *Bregmaceros* sp.. Solitary occurrences of *Bathyprius* sp., *Mugil* sp., and *Solenorhynchus* sp. are confined to this zone only.

Besides these characteristic taxa there also occur those which are typical of the entire upper bathy-pelagic assemblage, like: *Apostasis* sp., *Echeneis carpathica*, *Hemithyr-sites* sp., *Idrissia* sp., *Poyipnus* cf. *anteasteroides*, *Priacanthus* sp., and *Zeus* sp. The IPM3 Zone is dominated by long-lived taxa, like: *Clupea* sp., *Lepidopus* sp., *Polyipnus* sp., *Eomyctophum* sp., *Vinciguerria* sp., and *Serranus* sp., which are accompanied by fairly frequently occurring *Palaeorhynchus* sp. and *Vinciguerria distincta*. The remaining taxa are subordinate ones. One should take notice of the marked decline of *Palaeogadus* sp. and *Syngnathus* sp.

IPM4A Zone

The assemblage of this zone lists 40 taxa, including 8 representative ones. Among the latter, *Carpathospinosus* sp., *C. propheticus*, and *Centriscus* nov. sp. attain a considerable share, whereas *Caprovesposus* sp., *Forcipiger* sp., *Oligobalistes* sp., *Scorpaena* sp., and *Pseudoraniceps* sp. occur less frequently.

Fairly numerous are *Centriscus* sp. and *Antigonia* sp., each of them marking its presence in the basin two times only.

For the first time there occur, quite frequently, those taxa which will become characteristic of the higher part of the upper bathy-pelagic assemblage: *Syngnathus* sp. (typus A) and *Africentrum* sp., together with less frequent: *Eomyctophum* cf. *koraense*, *Holocentroides* sp. and *Zeus faber*. Also important are earlier-appearing taxa, like: *Hemithyr-sites* sp., *Capros* sp., and *Syngnathus incompletus*, as well as common taxa.

IPM4 Zone

The assemblage of this zone includes 43 generic and species taxa, including 7 representative ones. The latter are dominated by *Polyipnus sobnioviensis* and *Idrissia carpa-thica*, whereas *Priacanthus longispinus*, *Oligolactoria bu-biki*, *Equula?* sp. and *Alopecias* sp. appear rarely.

For the first time in this zone there occur: abundant *Eomyctophum menneri* and *Holocentroides moldavicus*, together with solitary specimens of *Alosa* cf. *sagorensis*, *Palaeomolva monstrata*, and *Vinciguerria merklini*. The dominant taxa include as well those known from other zones of the upper bathy-pelagic assemblage: *Eomyctophum* cf. *koraense*, *Africentrum* sp., *Idrissia* sp., and *Polyipnus* cf. *anteasteroides*, and the taxa occurring in many zones of the discussed time interval: *Eomyctophum* sp., *Polyipnus* sp., *Clupea* sp., *C. sardinites*, *Lepidopus* sp.

Of special importance is the last appearance in the basin of *Holosteus* sp. (1 specimen) and *Vinciguerria obscura*, although one cannot exclude that the latter has not been recognised among those specimens of *Vinciguerria* sp. which occur in higher-situated zones.

IPM5 Zone

This zone bears 38 (39?) taxa, including 4 representative ones: two dominant (*Carpathichtys polonicus* and *Carpathichthys* sp.) and two subordinate: *Syngnathus* sp. (typus B) and *Sphyraena* sp.. *Nessoramphus* sp. and *Acanthocy-bium* sp. appear for the first time in this zone, alongside with signal appearance (F_{EAD}) of *Argyropelecus* sp. and *Palaeogadus distinctus* which are characteristic of the IPM6 Zone.

Among taxa belonging to the upper bathy-pelagic assemblage, the dominant are: *Holocentroides moldavicus*, *Holocentroides* sp., *Africentrum* sp., *Idrissia* sp., *Zeus* sp., and *Syngnathus* sp. (typus A).

The assemblage bears a large amount of common taxa, like: *Clupea* sp., *Lepidopus* sp., *Eomyctophum* sp., *Palae-orhynchus* sp., and *Serranus* sp., whereas *Scorpaenoides* sp. attains here its climax.

Doubts as to the presence of *Kotlarczykia* sp. have been discussed at large in the preceding chapter: A new attempt...– IPM4B Zone.

IPM6 Zone

The fish assemblage of this zone is the richest one, including 3,276 specimens and 66 taxa. Eight taxa are confined solely to this zone, the most numerous being *Argyro-pelecus* sp. and the index taxon *Argyropelecus cosmovicii*, whereas *Paraberyx* sp., *P. bachoviensis*, *Archaeus* sp., *Capros medianus*, *Prohollandia avita*, *Protomyctophum* sp., and *Propteridium* sp. are less frequent.

The frequently occurring taxa include representatives of the upper bathy-pelagic assemblage, like: *Palaeogadus distinctus*, *Holocentroides moldavicus*, *Africentrum* sp., *Idrissia* sp., and *Hemithyr-sites* sp., as well as those which can be traced from the IPM2 Zone onwards: *Merluccius* sp. and *Syngnathus incompletus*. The bulk of biocoenosis of this

Fig. 16. Rarely occurring taxa, characteristic either for two neighbouring zones or for the upper bathypelagic assemblage: **A** – *Nessoramphus* sp. and **B** – *Acanthocybium* sp. (zones IPM 5 and IPM 6); **C** – *Palaeogadus intergerinus*; **D** – *P. carpathicus*; **E** – *Parasteindachneria oligocenica* (zones IPM 6 and IPM 7); **F** – *Onobrosomus* sp. (zones IPM 4A and IPM 6) and **G** – *Palaeomolva monstrata* (zones IPM 4 and IPM 6); **H** – representative of Psettoidea (Zone IPM 4)

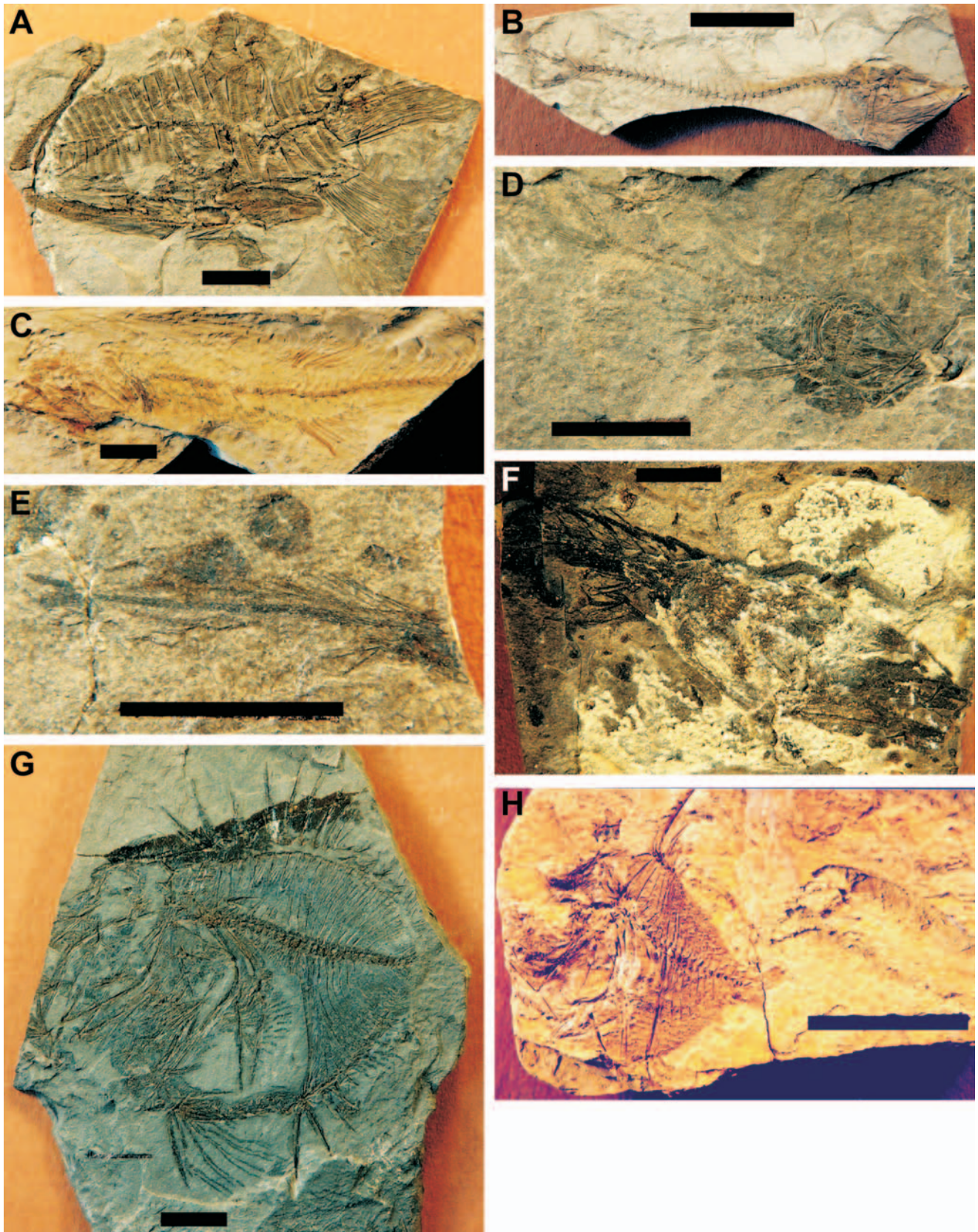
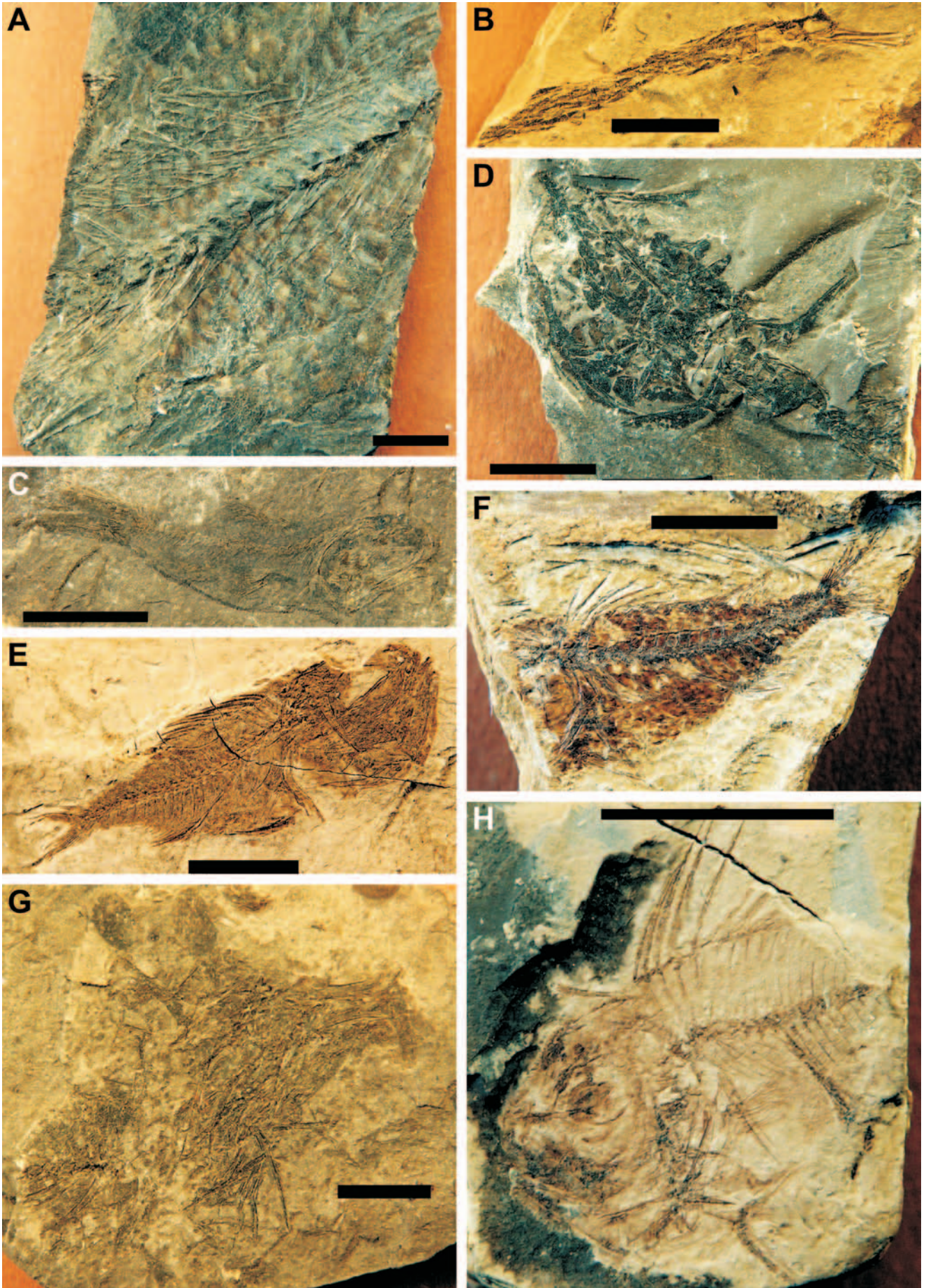
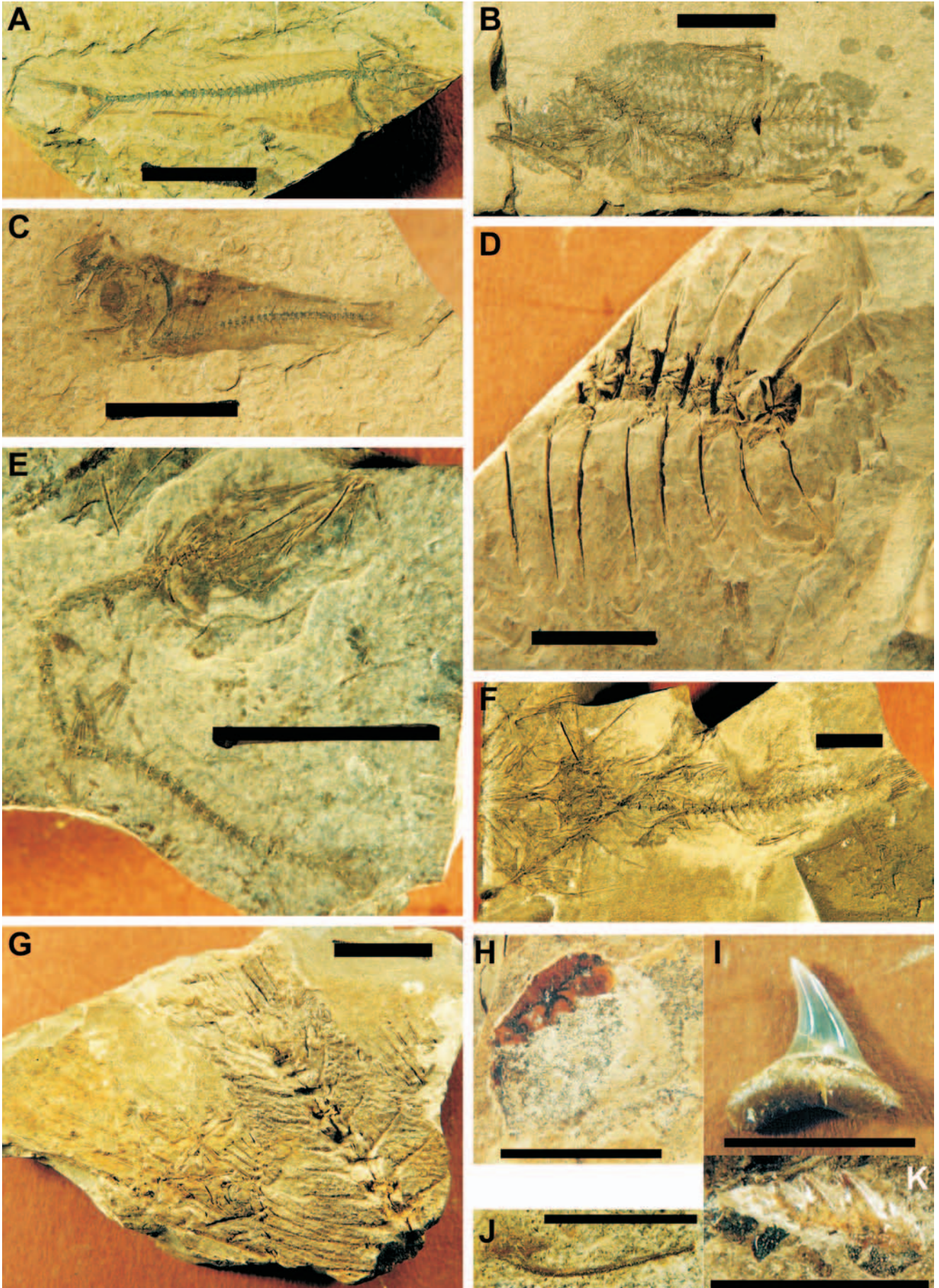


Fig. 17. Most representative taxa of the upper bathypelagic assemblage, not illustrated previously: **A** – *Echeneis carpathica*; **B** – *Idrissia* sp.; **C** – *Vinciguerria merklini*; **D** – *Polyipnus* cf. *anteasteroides*; **E** – *Hemithyrsites* sp.; **F** – *Thyrsitoides* sp.; **G** – *Zeus* sp.; **H** – *Antigonina* sp.

Fig. 18. Continued from Fig. 17: **A** – *Alosa* cf. *sagorensis*; **B** – *Syngnathus* sp., *typus A*; **C** – *Eomyctophum menneri*; **D** – *Palaeogadus distinctus*; **E** – *Holocentroides moldavicus*; **F** – *Africentrum* sp.; **G** – *Apostasis* sp.; **H** – *Priacanthus* sp.





zone is composed of long-lived taxa which found here optimal living conditions: *Lepidopus* sp., *Clupea* sp., *Syngnathus* sp., and – first of all – *Eomyctophum* sp. A marked proportion attain as well *Thyrsoideus* sp., *Serranus* sp., and *Vinciguerria* sp.

Besides representative taxa, numerous taxa known from previous zones tend to disappear in this zone. These include: *Antigonia* sp., *Zeus* sp., *Holocentroides* sp., *Alosa* cf. *sagorensis*, *Apostasis* sp., *Priacanthus* sp., *Polyipnus* cf. *anteasteroides*, *Syngnathus* sp. (typus A), and many others.

IPM7 Zone

The fish assemblage of this zone is for the first time a clearly impoverished one, including 29 taxa only. In previous zones, the number of taxa averaged around 40, except for the IPM6 Zone. This impoverishment is, in part, a result of the relatively small sample (452 specimens), although the dominant factor appears to be genuine disappearance of numerous taxa, including those very common in the IPM6 Zone, like *Argyropelecus* sp. and *A. cosmovicii*.

Exclusively in IPM7 Zone, a tooth of *Notidamus* sp. has been found. The assemblage is dominated by such common taxa, as: *Clupea* sp., *Lepidopus* sp., and *Syngnathus* sp.

The typical taxa of this zone include: dominating *Eomyctophum* sp. together with species *E. menneri*, as well as *Vinciguerria* sp., *Merluccius* sp., and *Idrissia* sp..

This zone includes already 20 taxa, including 11 known from the upper bathy-pelagic assemblage, which are represented by infrequent or solitary specimens. None of these taxa passes into the last zone.

INM1 Zone

A still poorer assemblage of this zone (11 taxa) is composed nearly in half of the representative taxa. These include: frequently represented *Leiognathus* cf. *minutus*, and less frequently occurring: *Caranx gracilis*, *Gobius* sp., *Merluccius errans*, and *M. hartensis*. No deep-water taxa have been found, although the pelagic ones are fairly numerous: *Clupea* sp., *Lepidopus* sp., and *Syngnathus* sp.

ECOSTRATIGRAPHY OF THE MENILITE-KROSNO SERIES (GROUP) IN THE POLISH CARPATHIANS

Classification of the collected material and determination of the extent of individual taxa presented in the previous chapter allows one to formally define the new ichthyofaunal zones and redefine previously-distinguished ones by taking into account: the zone type, determination of index

taxa, precise positioning of zonal boundaries, and determination of stratotypes.

The established correlation among exposures (Table 26) makes it possible to trace spatial distribution of zonal assemblages between the zones of the study area, already discussed in chapter: Lateral variability... and illustrated in Tables 27–34. Unlike the synthetic table presented in the previous chapter, Tables 27–34 include fish derived from supplementary exposures; hence, these two types of tables show a slightly different extent of some of the taxa. The absence of taxa from some zones can result from the lack of exposures bearing relevant fish specimens, whereas the lack of many taxa in a zone can point to insufficient sampling. Both these cases do not, however, testify to lateral disappearance of taxa in a biozone.

Redefinition of the *Scopeloides glarisianus* and *Eomyctophum limicola* (IPM1) Zone

An analysis of fish assemblages collected from new exposures (i.a., S₁, S₂) indicates that the two index taxa display analogous extent and reach as high as the top of the Dynów Marl Member. This zone is an assemblage zone. Taking into account that the upper zone boundary, presently situated at the top of the Dynów Marls, is poorly marked in the stratotype Jamna Dolna section, and that it has not been documented at Krępak (KIV; Table 5), it is proposed to chose exposure S₁ (up to the base of S_{1b}) at Straszydle (Fig. 6) as a stratotype of both the higher part of this zone (including the Dynów Marl Member) and of its upper boundary, which coincides with the lower boundary of the shale sequence of the Rudawka Tractonite Member.

The definition of the lower boundary of this zone remains unchanged; it is marked by the occurrence of either of the two index taxa. The formal boundary stratotype is located within the shale packet A of the Jamna Dolna Member (Fig. 6).

The lowermost portion of the Menilite Formation has not been sampled sufficiently enough to decide whether the lower boundary of the *S. glarisianus* Zone is confined to the base of the formation. At a few exposures (e.g. Kałolówka-KK₁, Ratny-RT), where the lowest layers of the Menilite shales of the Jamna Dolna and Siedliska members have been sampled, no index taxa have been found. There is, however, little evidence in favour of distinguishing a new zone like, for instance, *Vinciguerria talgiensis*. For practical reasons, the lower boundary of the IPM1 Zone can be temporarily associated with the first intercalation of brown shales which appears within the Globigerina Marl horizon, underlying the Menilite Formation. Therefore, the last mentioned taxon should be considered one of characteristic taxa of the IPM1 Zone (Fig. 20), alongside with *Palimphytes lanceolata*, *Scorpaenoides popovici*, and *Diaphus* sp. Taking

Fig. 19. Fish specimens of the Carpathian collection, provisionally distinguished as types, as well as isolated fish remains: **A** – Bathylagidae, typus *Melania*; **B** – Myctophidae, typus Giant II; **C** – Sternoptychidae, typus xz; **D** – Stromatoidei, typus Giant III; **E** – Salmoniformes?, typus xx; **F** – Perciformes, typus à la, à la; **G** – Teleostei, Genus indet, typus A; **H** – *Barbus* sp. (scale); **I** – *Alopecias* sp. (tooth); **J** – *Cetorhinus* sp. (filtrative process); **K** – *Notidamus* sp. (tooth)

Table 26

Classification of exposures of individual zones (I through VIII) into the respective ichthyofaunal zones

	VIII Jasło – Wisłok Wielki	VII Przysiętnica	VI Dobra – Temeszów- Mrzygłód	V Leszczawa-Hłudno	IV Borek-Błazowa	III Krepak	II Babice-Wola Węgierska	I Jamna Dolna- Kniażyce
INM-1				HP,ZH	HT			
IPM-7			KS ₁	HD ₃ HD ₁₊₂	B ₁₅ B ₂ B ₃ B ₅ B ₆ B _K KD KK ₂ PP	KII BR ₁ BR ₂	PB	DU ₁
IPM-6		PS ₁₀ PS _{8+8a+8b}	MR ₄ KS ₃	H ₁ H ₂ H ₇	B ₁ B _c B _a B ₄ B	BH ₁ BH ₂ BR ₁₀ BR ₄ BR ₅ BR ₆ KII ₁ KII _b KII _c KII _e	BP ₂	DU ₂ Ł ₃
IPM-5		PS ₁	SE ₁₊₂ SE ₁₊₃ SE _{II}			BR ₁₁ BR ₃₄ BH ₃ HB ₆ KIII		
IPM-4	SO G	PS _{3+3a} PS ₂ PS _{II} JZ _b	MR ₁ MR ₂ MR ₃ BK ₁	H ₁₁₉	ŁŁ ₁ BN ₇ BG	KI _{1+1a} KI		DU ₃ KN ₁ Ł _{1+1A}
IPM-4A		PS ₄ PS _{5+5a} PS _{6+6a}						DU ₄ KN ₄ Ł ₂
IPM-3		PS ₇ PS _{7A?}		L ₁		KIV ₄₊₅		
IPM-2	RR ₁₋₃ RO ₁ R ₁ R _{4-up} BB _{118, 104}	KL KR _{up} W WW	ST T ₁ DG D ₁ D _a	H ₃ H ₄ H ₅ H _{DS}	BE ₁ B _m BN ₃₊₄₊₅ BN _{IX-11} S ₃ HE	KI _G KIV ₁₋₃ BR ₄₃ BR ₄₅	WE _{up} BZ BP ₁ SR	J _{D-G} J ₃ J ₄
IPM-1	RR _{4bp} RK _{4a} RR _{4b} RO ₂	BO KR _{bp} BB _{iterat.} R _{4bp}	BK ₂ O ₁ O ₂ RT	N H ₁₃₂ H ₆ KC ₂	BW BN _{7a} C F HK ₂ KK ₁ LA P ₃ P ₆ S _{1,1a} S ₂ U	KI ₃ BR ₂₂ BR _{22a} HB ₁	WE _{bp} SK	J _{A-C} J ₁ J ₂ J _{pp}

into account the small number of specimens, it is hardly possible to decide whether these and other representative taxa of the IPM1 Zone will maintain their exclusive status, following the enlargement of fish collection derived from higher-situated zones.

The lower and upper boundaries of the IPM1 Zone coincide with analogous boundaries of the lower bathypelagic assemblage (LBA), typified by the presence of deep-water taxa, like: *Eomyctophum* sp., *Scopeloides* sp., *Vinciguerria* sp., and others.

The IPM1 Zone as well as LBA include the Siedliska, Jamna Dolna, Boryslav, Kotów, and Dynów members.

These members, except for the first and last one, frequently bear representatives of three species of *Centriscus*, what justifies distinguishing a concurrent-range-subzone (IPM1-C.SUB.) bearing index taxa of *Centriscus heinrichi*, *C. longispinus*, and *C. teleajensis*. Exposure at Jamna Dolna is the stratotype of this sub-zone and its boundaries.

Most probably, the LEADs of taxa *Scopeloides glarianus* and *Scopeloides* sp., as well as *Eomyctophum limicola* represent genuine LADs of those extinct forms which have never appeared within younger sediments.

The extent of index taxa is associated with five external zones; whereas in three internal zones these taxa are replaced by a representative taxon *Scopeloides* sp. The absence of index taxa in internal zones, alongside with the lack of common *Eomyctophum* sp. in zones VIII and VII can result from insufficient number of individuals within the collected samples. That was also the reason for the absence of index taxa of the *Centriscus* Subzone within internal zones. However, it is a well known fact that *Centriscus heinrichi* used to be found at Bóbrka and Lubatówka (zone VIII) within basal cherts of the Menilite Formation (Böhm, 1941).

Redefinition of the *Glossanodon musceli* and *Palaeogadus simionescui* (IPM2) Zone

This zone is characterised by frequent occurrence of the two index taxa. Recently confirmed appearance of the first taxon, also within the IPM1 Zone (A. Jerzmańska described this taxon in the upper part of the Dynów Marl Mbr at S₁ and S₂ at Straszydło, as well as in a rock fragment derived from the Dynów Marls, found in a submarine slump at exposure BN_{7A}) enables one to describe that variety of this zone as a concurrent-range zone (Fig. 20). The accompanying taxa, confined nearly exclusively to this zone, are represented by *Eophycis jammensis* and *Eophycis* sp., and – occasionally – *Palaeogadus abbreviatus*, *Hemiramphus jerzyi* and *Pomolobus* sp. The stratotype is composed of a bed sequence of the Rudawka Member at exposure Jamna D-G (counting from the layer D₁ upwards) in the lower part, and a sequence of the Borek Nowy Member at Krępak IV (comprised between the layers IV₁ and IV₃) in the upper part (Fig. 6).

The second ichthyofaunal zone is linked with the first one; the lower boundary of the former coincides with the upper boundary of the latter, whereas the boundary stratotype is the same. The upper boundary of the IPM2 Zone is

marked by LEAD *Glossanodon musceli* and the termination of massive occurrence of *Palaeogadus simionescui*, as well as by disappearance of accompanying taxa. The upper boundary stratotype of this zone can be traced at Krępak IV between layers KIV₃ and KIV₄ and coincides with the upper boundary of the Borek Nowy Member. Therefore, within the Skole, Boryslav-Pokuttya, and Subsilesian units, the IPM2 Zone includes several lithostratigraphic units, like the Rudawka, Futoma and Borek Nowy members, whereas in the Silesian Unit it comprises the entire bed sequence overlying the Dynów Member.

The lower and upper boundaries of the IPM2 Zone coincide with analogous boundaries of the neritic-sublittoral assemblage (NSLA) which is characterised by overwhelming presence of shallow-water fish.

It is proposed to distinguish a characteristic layer of the lower part of the IPM2 Zone (E₁ at Jamna Dolna D-G), including *Trachinus minutus* and *Hipposyngnathus neriticus*, as a sub-zone bearing index taxon *T. minutus* (IPM2-T.SUB.) whose stratotype is situated at that exposure and layer. The solitary occurrence of such a layer within the section represents an event which left its trace (cf. Table 28), apart from Jamna Dolna (zone I), also at Leszczawa – L (zone V) and, probably, at Wola Węgierska – WE_{up} (zone II), where a specimen of uncertain *Trachinus?* sp. has been found.

It can be safely concluded that the LEADs of characteristic taxa *Glossanodon musceli*, *Trachinus minutus*, *Hipposyngnathus neriticus*, and *Eophycis jammensis*, and perhaps some others mark the genuine extinction of these forms at that time.

The distribution of index taxa *Glossanodon musceli* and *Palaeogadus simionescui* shows this time gaps in the outer zones (Table 28), although these forms are replaced by *Glossanodon* sp. and *Palaeogadus* sp. Still broader gaps are confined to *Eophycis jammensis*, *Eophycis* sp., and *Holoosteus* sp. Such a situation reflects the availability of exposures in some zones and preferences of their explorators.

Redefinition of the *Horbatshia brevis* (= *Polyipnus brevis*), *Kotlarczykia bathybia*, and *Bregmaceros filamentosus* (IPM3) Zone

In this chapter, extending beyond the problems of documentation of collection's description and characteristics of taxa distribution, a new name of the first index taxon has been used. This name was originally proposed by A. Jerzmańska and introduced by Prokofiev (2002a). This will prevent further revision of the described stratigraphic unit.

The third ichthyozone was distinguished on the basis of time-range of the first taxon and the two co-existing ones. The IPM3 Zone is a concurrent-range zone (Fig. 20).

Its stratotype is represented by the upper part of exposure KIV at Krępak, composed of thin-bedded sandstones intercalated by green and brown shales, and distinguished as the Krępak Member, overlying the Borek Nowy Member (Fig. 6; layers: 4 – 4_y).

The IPM3 Zone is linked with IPM2 Zone. The upper boundary of the third zone has never been determined pre-

ZONE		SUBZONE/EVENT		SIGNIFICANT ACCOMPANYING TAXA	
Symbol	Stratotype	Other representative taxa Index fossils	Index fossils		
upper neritic sublittoral	Harta (HT) Huta Poreby (HP, ZH)	Merluccius errans Caranx gracilis	INM1-L	<i>Gobius</i> sp. <i>Palaeogadus distinctus</i> <i>Glyptothidium</i> sp. <i>Parasteindachnena</i> olig. <i>Palaeogadus intergenus</i> <i>Palaeogadus carpathicus</i>	
					<i>Merluccius hartensis</i> <i>Leiognathus</i> cf. <i>minutus</i>
upper bathy- pelagic	Krepek (KII)	Eomycotophum menneri	IPM6-S	<i>Merluccius</i> sp. <i>Hemithyrstes</i> sp. <i>Itrisia</i> sp. <i>Echeneis carpathica</i> <i>Polyipnus</i> cf. <i>anteasteroides</i> <i>Apostasis</i> sp. <i>Zeus</i> sp. <i>Priacanthus</i> sp. <i>Antigonia</i> sp. <i>Eomycotophum</i> cf. <i>koraeense</i> <i>Atracentrus</i> sp. <i>Syngnathus</i> (typus A) <i>Holocentroides</i> sp. <i>Holocentroides moldavicus</i> <i>Eomycotophum menneri</i> <i>Alosa</i> cf. <i>sagorensis</i> <i>Nessoramphus</i> sp.	
					<i>Protomycotophum</i> sp. <i>Archeus</i> sp. <i>Prohollandia avita</i> <i>Capros medianus</i> <i>Paraberyx bachoviensis</i> <i>Argyropelecus cosmovicii</i>
					<i>Syngnathus incompletus</i>
upper bathy- pelagic	Krepek (KIII)	Syngnathus sp. (typus B) Carpathichthys polonicus	IPM5	<i>Merluccius</i> sp. <i>Hemithyrstes</i> sp. <i>Itrisia</i> sp. <i>Echeneis carpathica</i> <i>Polyipnus</i> cf. <i>anteasteroides</i> <i>Apostasis</i> sp. <i>Zeus</i> sp. <i>Priacanthus</i> sp. <i>Antigonia</i> sp. <i>Eomycotophum</i> cf. <i>koraeense</i> <i>Atracentrus</i> sp. <i>Syngnathus</i> (typus A) <i>Holocentroides</i> sp. <i>Holocentroides moldavicus</i> <i>Eomycotophum menneri</i> <i>Alosa</i> cf. <i>sagorensis</i> <i>Nessoramphus</i> sp.	
					<i>Priacanthus longispinus</i> <i>Itrissia carpathica</i> <i>Polyipnus sobnioviensis</i>
lower neritic sublittoral	Przysietnica (PS _{6,5})	Forcipiger sp. Antigonia sp. Centriciscus nov. sp. Carpathospinosus <i>propheticus</i>	IPM4A	<i>Merluccius</i> sp. <i>Hemithyrstes</i> sp. <i>Itrisia</i> sp. <i>Echeneis carpathica</i> <i>Polyipnus</i> cf. <i>anteasteroides</i> <i>Apostasis</i> sp. <i>Zeus</i> sp. <i>Priacanthus</i> sp. <i>Antigonia</i> sp. <i>Eomycotophum</i> cf. <i>koraeense</i> <i>Atracentrus</i> sp. <i>Syngnathus</i> (typus A) <i>Holocentroides</i> sp. <i>Holocentroides moldavicus</i> <i>Eomycotophum menneri</i> <i>Alosa</i> cf. <i>sagorensis</i> <i>Nessoramphus</i> sp.	
					2nd Centriciscus event
lower neritic sublittoral	Krepek (KIV _{4-4b})	Bregmaceros filamentosus Kotlarczykia bathybia Horbatshia brevis (=Polyipnus brevis)	IPM3	<i>Thyrstoides</i>	
lower neritic sublittoral	Jamna (JD-G) Krepek (KIV ₁₋₃)	Hemiramphus Jerzyi Eophycis jammensis Palaeogadus simionescui Glossanodon muscelfi	IPM2-T		
					Trachinus event <i>Trachinus minutus</i>
lower bathy- pelagic	Jamna (JA-C) Straszyle (S ₁)	Palimphyes lanceolata Vinciguerria telgensis Eomycotophum limicola Scopeloides glaritanus	IPM1-C		
					1st Centriciscus event <i>Centriciscus teleajensis</i> <i>Centriciscus longispinus</i> <i>Centriciscus heinrichi</i>

Fig. 20. Ichthyofaunal zonation of the Menilite-Krosno Series in the Polish Carpathians. Double line separates independent zones

cisely; most probably, it occurs already below layer IV₅, since the latter appears to be devoid of index taxa. The lower boundary of this zone coincides with the lower boundary of the upper bathy-pelagic assemblage (UBA).

L_{EAD} *Horbatshia brevis* probably marks the extinction of this taxon. The index taxa of this ichthyozone have also been found at Leszczawa (exposure L₁, without *B. filamentosus*) in zone V, and at Przysietnica (exposure PS₇) in zone VII (Table 29). The first index taxon was originally found in the Eastern Carpathians at Delatyn, in the Skole Unit (Horbatsh, 1961).

Definition of the *Carpathospinosus propheticus* and *Centriscus* nov. sp. (IPM4A) Zone

The IPM4A assemblage zone is characterised, apart from index taxa, by the accompanying ones: *Carpathospinosus* sp., *Centriscus* sp., and *Antigonina* sp. (local acme for the last taxon), as well as by the *Centriscus* event taxa. It is hardly possible to predict whether other, poorly represented, characteristic taxa will maintain their status owing to further exploitation and enlargement of fish collections derived from older and younger zones.

The stratotype is located at Przysietnica in exposure PS₅₊₆, where a ca. 13-m-thick sequence of alternating brown and grey shales, bearing a horizon of laminated limestones of the Wujskie Limestone Horizon occurs.

The lower boundary of this ichthyozone should be associated with the first appearance of *C. propheticus* in limestone layers, while the upper boundary should be linked with the uppermost occurrence of *Centriscus* nov. sp. in layer 12 (cf. Table 6). Since the beds underlying and overlying exposure PS₅₊₆ have not been explored, it is impossible to decide whether zonal boundaries are really located within indicated layers or not.

The obtained results indicate that the zone IPM4A is the first independent zone in the UBA (Fig. 20). The appearance of *Bregmaceros filamentosus* in layer 58, shortly below finely laminated limestones, is not accompanied by main index taxa of the IPM 3 Zone. Most probably, a gap occurs between zones IPM3 and IPM4A. On the other hand, no coincidence between the above-defined upper boundary of the IPM4A Zone and the lower boundary of the IPM4 Zone has been found.

Due to practical reasons, it is convenient to associate the IPM4 Zone with a sequence of layers which is comprised between the Wujskie Limestone Horizon and the Jasło Limestone Horizon. In such an approach, fish collected from interzone intervals (lower layers of exposure PS₆, exposure PS₄) are included into the IPM4A Zone' assemblage.

It is highly probable that L_{EAD} *Carpathospinosus propheticus* is associated with the extinction of this taxon. The IPM4A Zone has been identified exclusively in zone VII (Table 30), and only some taxa of its assemblage have been found in zone I.

Redefinition of the *Polyipnus sobniowiensis* (IPM4) Zone

This taxon-range zone is closely associated with the Jasło Limestone Horizon which, at Przysietnica, builds the

upper level of finely-laminated limestones. Exposure at Łubno-Łazek (ŁŁ₁; Jerzmańska & Jucha, 1963) was chosen as the stratotype of this zone and its boundaries (Kotlarczyk & Jerzmańska, 1976). Species *Idrissia carpathica* and *Priacanthus longispinus* display a similar extent (Fig. 20), although widespread distribution of these two genera in the UBA requires a great deal of caution when attempting at their use as index taxa.

Both boundaries of this relatively narrow zone are marked by F_{EAD} and L_{EAD} of the index taxon. The zone shows a wide, well-documented distribution (Fig. 30), similar to that of a chronohorizon. The zone was also traced in the stratotype area of the Brzuska syncline. The Jasło Limestone Horizon rarely lacks the index taxon; hence, its absence from the zone I is surprising. It is worth noting that the described zone is the only one of the upper bathy-pelagic assemblage which was documented in the Krosno Formation of the Silesian Unit.

The IPM4 Zone is not linked with the two neighbouring ones. The index taxa-free fish assemblage of the IPM4A – IPM4 interzone was included into the IPM4A Zone, whereas that of the IPM4-IPM5 interzone became assigned at individual exposures to either older (e.g. Krępak KI₁), or younger (e.g. Bachów BH₃) zones.

Redefinition of the *Carpathichthys polonicus* (IPM5) Zone

This local taxon-range zone has its stratotype section located at Krępak (exposure KIII), while the presently accessible section (since the time of establishing a nature reserve at Krępak), most suitable for detailed studies, occurs in the upper part of exposure BH₃ at Bachów. The fish assemblage of this zone is comprised in a sequence of brown and sometimes green shales, and predominantly thin-bedded sandstones. Some of these sandstones originated due to cohesive sand-muddy flows (sandstones of the Jawornik Ruski type), whereas others represent a facies of the Krosno sandstones.

The upper and lower boundaries of the zone are marked, respectively, by F_{EAD} and L_{EAD} of *C. polonicus* (Fig. 20). In the stratotype section, these boundaries are associated with layers 2 and 6 (Fig. 6: KIII; Table 7), whereas at exposure BH₃ they are confined to layers Ja and Ju/Ja, as well as – probably – layer E (bearing a representative of Alepocephalidae; Table 8). Both these sections, however, are devoid of characteristic lithological marker horizons that would coincide with the boundaries. In the stratotype section, the discussed zone can be easily identified behind a road bend (cf. fig. A.32 in: Kotlarczyk & Jerzmańska, 1988b).

The first zonation scheme (Fig. 10) accepted families of Alepocephalidae and Nessoramphidae as index taxa. Later, it was found out that the latter family existed in the basin between the fourth and sixth ichthyozones, and that the material representing both the IPM6 Zone and IPM4-IPM5 interzone (included into the fifth zone) contains *Nessoramphus* sp. (cf. Table 31). These circumstances and the lack of co-existence in the same bed sequence of *Nessoramphus* sp. and *C. polonicus* (the lower part of Table 31 represents the

lower portions of exposure BH₃) make the acknowledgement of *Nessoramphus* sp. as the second index taxon of the IPM5 Zone redundant.

The hitherto-recognised distribution of the IPM5 Zone is restricted to three zones (Table 31) and 10 exposures (Table 26).

Redefinition of the *Argyropelecus cosmovicii* (partim *Argyropelecus* sp.) (IPM6) Zone

The index fossil of this taxon-range-zone, *Argyropelecus cosmovicii*, was unfortunately determined by A. Jerzmańska on the basis of infrequent specimens derived from two exposures only: Babice-Połanki (BP₂ – 2 layers) and Bachów (BH₁ – 2 layers), situated in the Skole Unit, and at an unidentified exposure at Przysietnica (PSO) in the Sub-silesian Unit (cf. Table 32). On the other hand, exposures of nearly all zones of this ichthyozone frequently bear fish specimens labelled as *Argyropelecus*. This term typifies a joint group in which some specimens tend to reveal properties of the species *A. cosmovicii* (see chapter: Composition of ichthyofauna). Waiting for a revision of specimens of this group, the extent of *Argyropelecus* sp. occurring in the stratotype Krępak section has been acknowledged as equivalent of the range of the IPM6 Zone.

This stratotype includes exposures extending between KII_e – KII_b and KII₂ (Fig. 4: K-HB, Table 9), in which the lower part of the Korzeniówka Member, representing the upper part of the Menilite Formation (the so-called upper Menilite beds in SKU), is exposed. The stratotype exposures display brown, sometimes marly Menilite shales including sandstone intercalations of the Jawornik Ruski type, Kliwa sandstones, calcareous sandstones of the Kliwa-Krosno type, sometimes green shales, and rare thin-bedded cherts (Fig. 6).

The accompanying taxa, occurring in minor quantities and confined exclusively to zones III and IV of this Zone, include: *Paraberyx bachoviensis* and *Paraberyx* sp. (III), *Capros medianus* (III–IV), *Prohollandia avita* (IV), *Archeus* sp. (III), and *Protomyctophum* sp. (Table 32). The lower boundary of this zone, marked by the onset of systematic, persistent appearance of *Argyropelecus* sp., is not linked with the IPM5 Zone, whereas the upper boundary is at the same time the lower boundary of the IPM7 Zone (Fig. 20).

Among the three observed occurrences of *Syngnathus incompletus* in the basin (IPM2, IPM4A-4?, IPM6-7? zones), the most important one is undoubtedly associated with the IPM6 Zone (Tables 25, 32). This implies a possibility of using this taxon as the second index taxon (already proposed by Kotlarczyk & Jerzmańska, 1988a), and defining the zone as an assemblage zone. However, the existing data are not sufficient enough to determine the genuine position of the boundaries of the epibole taxon within the zone. Geological setting of exposures at Babice-Połanki (BP₂), Przysietnica (PS₈) and Bachów (BH₁) appears to indicate a narrow range of epiboles. This fact was the basis of distinguishing of the *S. incompletus* sub-zone (IPM6-S.SUB.) within the IPM6 Zone (Kotlarczyk & Jerzmańska, 1976), with its stratotype at exposure BH₁.

The reconstruction of the extent of taxon *S. incompletus* and re-definition of the sub-zone comprising this taxon will not be possible until a revision of fish collected at exposures of the IPM6 Zone and classified into the joint group *Syngnathus* is performed.

It seems likely that the LEADs of *Argyropelecus cosmovicii*, *Paraberyx bachoviensis*, *Prohollandia avita*, and *Archeus* sp. mark the actual extinction of these forms.

Definition of the *Eomyctophum menneri* (IPM7) Zone

The definition of this zone, presented below, is somewhat biased due to relatively poor recognition of its fish assemblage. Apart from accidental appearance of *Notidanus* sp., no representative taxa have been identified in the assemblage which is typical of the upper part of the upper bathy-pelagic assemblage (UBA). The IPM7 Zone is the uppermost one within this assemblage; therefore, selection of an index taxon from the representatives of that ichthyocoenosis appears to be fully justified.

Among deep-water fish, *Eomyctophum* sp. occurs abundantly and commonly in all the zones, whereas *Idrissia* sp. and *Vinciguerrria* sp. are to be found in selected zones only. On the other hand, numerous taxa are represented by so small numbers of specimens that they cannot be considered index ones (Table 33).

In these circumstances, it was decided to define provisionally the new zone as a successive last appearance zone, bearing an index taxon *Eomyctophum menneri* (Fig. 20). This taxon also occurs in the underlying IPM6 Zone, together with its index taxon *Argyropelecus cosmovicii* and *Argyropelecus* sp., as well as other proper taxa of the IPM6 Zone. Hence, the lower boundary of the IPM7 Zone is marked by the uppermost extent of *A. cosmovicii* and *Argyropelecus* sp. The upper boundary, in turn, is defined by disappearance of the index taxon and of other fossil fishes from the stratigraphic section at the transition between the Menilite and Krosno formations. Therefore, the described unit is linked with the underlying zone only.

The characteristic taxa of this zone, despite negligible proportions, include: *Glyptophidium* sp., *Parasteindachneria oligocenica*, and three species of *Palaeogadus* which occur in the upper part of the Menilite Formation.

The stratotype of this zone is exposure KII at Krępak (Fig. 6, Table 9), which includes a portion of the Korzeniówka Member, ca. 25 m thick, situated above a packet representing the IPM6 Zone (exposures: KII_e – KII₂; see Fig. 4: K-HB).

This ichthyozone has been recognised in the Skole Unit only.

Redefinition of the *Caranx gracilis* and *Merluccius errans* (INM1) Zone

The only Miocene assemblage zone occurs in the uppermost portion of the flysch sequence of the Polish Outer Carpathians. It was determined basing on similar range of the two taxa considered as index ones. The composite stratotype comprises exposures of a portion of the Krosno Formation situated close to the Dobrzanka Tuff Horizon (t. V)

at Harta (HT) (Fig. 4: BN, Fig. 6), the lower part of the Leszczawka Diatomite Member at Huta Poręby (HP) (Fig. 4: L, Fig. 6), and a layer of laminated Jasło-type limestones, occurring as dismembered fragments in a submarine slump in the Zahuty Stream (ZH), at Huta Poręby.

A large portion of the Leszczawka Diatomite Member represents an olistostrome. The submarine slump, including laminated limestones, occurs within a sequence of marls and calcareous shales of the Krosno type below the highest packet of diatomaceous rocks (Fig. 4: L). The age of limestones can be estimated, basing on different pieces of evidence, as older than that of the slump, but not much older than the Leszczawka Diatomite Horizon. This enables one to include a specimen of *Caranx gracilis*, found in limestones, to the ichthyo-thanatocoenosis that occurs in the Leszczawka Member.

Stratigraphic separation between exposures HT and ZH is fairly large, amounting to ca. 600 m. Most of this distance spans a sequence of normal flysch, while olistostrome deposits are not so thick (Fig. 3:BN-HT, L-HP). Therefore, the time interval necessary for the development of fish assemblage of this zone was not very long, probably lasting no more than ca. 2 m.y..

Stratotype exposures are situated in closely-spaced structures; therefore, the presently recognised extent of this ichthyozone is restricted to the two distinguished zones: IV and V (Table 34).

The IPM7 Zone represents an independent unit. The duration of the barren interzone *Eomyctophum menneri* – *Caranx gracilis* & *Merluccius errans* can be estimated at ca. 3–3.5 Ma.

Fairly numerous occurrences of *Leiognathus* cf. *minutus* and the appearance of a new species *Merluccius hartensis* at Harta (HT) enables one to distinguish the Subzone INM1-L.SUB., including both the above taxa as index fossils (Fig. 20).

An alternative solution, consisting in creation of the INM1 Assemblage Zone bearing index taxa of *Leiognathus* cf. *minutus* and *Merluccius hartensis*, as well as the INM2 Partial-Range Zone with *Caranx gracilis* or *Merluccius errans*, is not sufficiently justified by the presently available number of assemblages and sites.

PALAEOECOLOGY OF PALAEOGENE AND NEOGENE FISH IN THE POLISH OUTER CARPATHIAN BASIN

The first part of this chapter summarizes literature data pertaining to palaeoecology and palaeobathymetry of those fish genera and species which are included in the collection housed at the Department of Palaeozoology. The second part, in turn, deals with ecological characteristics of those fish assemblages which occur in the distinguished ecostratigraphic zones.

Palaeoecological analysis does not always lead to unequivocal solutions. One should take into account that not all families have their representatives living exclusively in one, strictly defined ecological environment, like, for instance, deep-water pelagic or deep-water benthic-pelagic ones. A

common feature is that some genera of the same family inhabit one biotope, while the remaining ones are confined to another biotope (cf. data concerning Myctophidae, in: Parin, 1988 – tables 3, 4). The same applies – to a certain degree – to different species of one genus. For instance, most species of the genus *Syngnathus* prefer near-shore environment, and one species of this genus is a pelagic one. In such cases, fish specimens identified to the level of family or genus do not provide precise ecological constraints.

The ichthyocoenosis of the Oligocene ocean was largely comparable to that of recent oceans (Gaudant, 1979). The collection studied includes only two families (Euzaphlegidae, Palaeorhynchidae) known exclusively from fossil material, and yet 27 extinct genera. Palaeoecological environment of the latter can only be inferred basing on their proximity of blood to the present-day genera, although this kind of reasoning requires a great deal of caution.

For the purpose of this work, the following ichthyocoenoses have been distinguished: pelagic, benthic-pelagic and bottom (demersal), as well as shallow-water neritic, and specific – reef ones. In many cases, it is also possible to apply a more detailed subdivision based on bathymetric zones.

The following ecological fish assemblages, marked by appropriate acronyms, have been distinguished:

EP – epipelagic, dwelling ocean waters down to a depth of 200 m (150 m);

MP – mesopelagic, dwelling a depth interval between 200 m and 1,100 m (or 150 m to 2,000 m);

BP – bathypelagic, dwelling still deeper waters, down to 4,000 m (although some fish can occur at shallower depths);

MB – meso-bathypelagic, dwelling both the above two zones;

BEP – benthic-pelagic, dwelling near-bottom waters to ca. 100 m above the bottom, and below the continental shelf break (without subdivision into meso- and bathy-zones);

BD + D – benthic, occurring at and close to the bottom, including:

D – demersal, buried, occurring at the bottom and shortly above it in the shallow-water zone;

BD – bathy-demersal, dwelling as in D, although upon continental slope or the slopes of submarine ridges and mounts;

N – neritic, dwelling supra-shelf waters between the surface and a depth of 200 m, including littoral ones;

R – associated with reef environment;

N + R – shallow-water, associated with the two previous environments.

These acronyms denote affiliation of individual fish families and genera to an appropriate ecological assemblage. Sign † marks extinct taxa.

Palaeoecology of fish families and genera

Order: LAMNIFORMES (EP, MP) (IPM 1, 4A, 4, 5)

Family: ALOPIIDAE –resher sharks (EP, MP) (IPM 4)

Genus: *Alopecias* (*Alopias*) Rafinesque, 1810 (EP, MP)

Alopecias sp. (*Alopias*, acc. to Nelson, 1994) (IPM 4).

These are oceanic sharks, dwelling a depth range of 0–550 m, known from subtropical waters. The present-day forms include lit-

toral, epipelagic, and those living far from the shoreline. Young individuals occur near shores or in bays (Parin, 1988; Weitzman, 1997; Froese & Pauly, 2004).

Family: CETORHINIDAE – basking sharks (EP) (IPM 1, 4, 5)
Genus: *Cetorhinus* Blainville, 1816 (EP)
Cetorhinus sp. (IPM 1, 4, 5).

Representatives of this genus are planktonivorous, migrating oceanic sharks. Recent fauna includes only one species, second in size among sharks. Depth range 0–570 m. These are epipelagic and pelagic, oceanodromic sharks, preferring moderate climate; occur close to continental or insular coasts. They usually move slowly near the surface, in groups numbering 3–4 individuals, although clusters exceeding 100 specimens have also been spotted. They are to be found in deeper waters in winter times (Froese & Pauly, 2004).

Order: HEXANCHIFORMES – (BD + D,R) (IPM 7)

Family: HEXANCHIDAE – cow sharks (BD + D, R) (IPM 7)
Genus: *Hexanchus* Rafinesque, 1810 (= *Notidamus* Cuvier, 1816) (BD + D)
Notidamus sp. (IPM 7).

Depth range 0–2,000 m. Recent representatives of this genus include demersal, bathy-demersal, marine forms. These are oceanodromic sharks, most of them dwelling upon continental slope, whereas other occur upon the shelf and shallower waters (coral reefs), as well as near-shore places. They occur in deep waters of the subtropical zone. Deep-water forms move at night into shallower depths (Weitzman, 1997; Froese & Pauly, 2004).

Order: ANGUILLIFORMES (BP, BD + D)
(IPM 3, 4A, 4, 5, 6, 7)

Family: DERICHTHYIDAE (NESSORHAMPHIDAE)
– longneck eels (BP)(IPM 4, 5, 6)

Recent representatives of this family are exclusively marine, bathypelagic forms, dwelling waters of deep-water climate of depths between 500 m and 2,000 m (Parin, 1988; Weitzman, 1997; Froese & Pauly, 2004).

Genus: *Nessorhamphus* Schmidt, 1931 (BP)
Nessorhamphus sp. (IPM 5, 6).

These are bathypelagic (0–1,800 m) marine fish, preferring deep-water climate (Weitzman, 1997; Froese & Pauly, 2004).

Order: CLUPEIFORMES (EP) (IPM 1, 2, 3, 4A, 4, 5, 6, 7,
INM 1)

Family: CLUPEIDAE – herrings (EP) (IPM 1, 2, 3, 4A, 4, 5, 6, 7,
INM 1)

Genus: *Clupea* Linnaeus, 1758 (EP)
Clupea sardinites Heckel, 1850 (IPM 1, 2, 3, 4, 5, 6)
Clupea sp. (IPM 1, 2, 3, 4A, 4, 5, 6, 7, INM 1)

These oceanodromic, brackish and marine forms occur in pelagic waters, up to 200 m deep, of moderate to subtropical climate. They tend to form shoals in near-shore waters; during the daylight they stay in deeper waters and come closer to the surface at night (Froese & Pauly, 2004).

Genus: *Alosa* Linck, 1790 (EP)
†*Alosa* cf. *sagorensis* Steindachner, 1863 (IPM 4, 6)
Alosa sp. (IPM 1, 2, 3, 4A, 4, 5, 6, 7, INM 1)

Depth range: 0–145 m; climate: moderate to subtropical. These are epipelagic, anadromic fish that dwell fresh, brackish, and marine waters. They spend their spawning season either in rivers or in brackish waters. Recent species can spend winter in open waters, coming back to littoral waters in spring. They tend to form shoals (Szymczyk, 1978, 1979; Froese & Pauly, 2004).

Genus: *Pomolobus* Rafinesque, 1820 (EP)
Pomolobus sp. (IPM 2)

Depth range: 0–145 m (epipelagic); occurrence: moderate to subtropical climatic zones. These are pelagic, anadromic fish; can dwell fresh, brackish, or marine waters. They spend their spawning season either in rivers or in brackish waters. Recent species can migrate in winter time into open waters, coming back to the littoral ones at spring. They tend to form shoals (Froese & Pauly, 2004).

Order: CYPRINIFORMES (BEP) (IPM 1)
Family CYPRINIDAE – minnows (BEP) (IPM 1)
Genus: *Barbus* Cuvier, 1817 (BEP)
Barbus sp. (IPM 1).

Recent representatives of barbels are benthopelagic, freshwater, and brackish fish that can dwell in moderate through subtropical climatic zones. They usually do not occur at depths exceeding 10 m, at a rocky bottom (Froese & Pauly, 2004).

Order: OSMERIFORMES (BEP, BP, BD) (IPM 1, 2, 3, 4A, 4, 5,
6, 7)

Family: ARGENTINIDAE – argentines (BP, BEP, BD, D)
(IPM 1, 2)

Genus: *Glossanodon* Guichenot, 1867 (BEP, BP, BD)
†*Glossanodon musceli* (Pauca, 1929), IPM 2 – index species
Glossanodon sp. (IPM 1, 2)

Depth range: 140–1,400 m (Froese & Pauly, 2004), or 70–1,000 m (Weitzman, 1997) (benthopelagic). These are benthopelagic, marine, deep-water fish, preferring moderate to tropical climate, dwelling close to the substratum (also a stony one), or within sandy or silty bottom. Frequently occur upon continental slope or off the shelf break (Jerzmańska, 1967, 1968; Ciobanu, 1977; Parin, 1988; Weitzman, 1997; Froese & Pauly, 2004).

Family: BATHYLAGIDAE – deep-sea smelts (BP) (IPM 1, 2,
4A, 4, 5, 6, 7)

These are deep-water, bathypelagic fish of a wide depth range (0–7,700 m; Froese & Pauly, 2004; or 0–3,600 m; Weitzman, 1997), exclusively marine, feeding on crustaceans and plankton; living either in small shoals or as solitary individuals (Parin, 1988; Froese & Pauly, 2004).

Genus: †*Idrissia* Arambourg, 1954 (BP)
†*Idrissia carpathica* Jerzmańska, 1960 (IPM 4)
†*Idrissia* sp. (IPM 3, 4A, 4, 5, 6, 7)

Photophores are absent. Bathypelagic, marine (0–5,000m; occurring most frequently down to 2,000 m) forms, preferring deep-water climate (Froese & Pauly, 2004). This genus resembles that of contemporaneous *Ichthyococcus* Bonaparte, 1840 (Jerzmańska 1960).

Family: ALEPOCEPHALIDAE – slickheads (BEP) (IPM 5, 6)
Genus: †*Carpathichthys* Jerzmańska, 1979 (BEP)
†*Carpathichthys polonicus* Jerzmańska, 1979, IPM 5 – index species
†*Carpathichthys* sp. (IPM 5)

Depth range: 500–2,100 m (benthopelagic), probably occur also in deeper waters. These are benthopelagic, marine forms known from deep-water and tropical climate (Jerzmańska, 1979; Parin, 1988; Froese & Pauly, 2004).

Genus: *Bathyprius* Marshall, 1966 (BP)
Bathyprius sp. (IPM 3).

These are deep-water, bathypelagic, marine fish, living at depths of 100 m to 3,200 m (Froese & Pauly, 2004; Parin 1988), or 1,100 m to 2,100 m (Weitzman, 1997).

Order: SALMONIFORMES (EP, BEP) (IPM 1, 3, 4A, 4, 5, 6, 7)

Fishes of moderate climate, occurring in the Northern Hemisphere. These are marine, epipelagic, benthopelagic, anadromic, fresh-water or brackish forms (Froese & Pauly, 2004).

Order: STOMIIFORMES (MB) (IPM 1, 3, 4A, 4, 5, 6, 7)

Family: GONOSTOMATIDAE – bristlemouths (MB, EP) (IPM 1, 3, 4A, 4, 5, 6, 7)

Genus: †*Scopeloides* Wettstein, 1886 (MB)

†*Scopeloides glarisianus* (Agassiz, 1844), IPM 1 – index species
†*Scopeloides* sp. (IPM 1)

Depth range: 25–3,385 m, usually 200–700 m. This is a bathypelagic, marine species, whose related, recent genera are able to migrate vertically throughout the day: dwelling shallow waters at night, and deeper ones during the daylight. Larger specimens prefer deeper waters. Deep-water climate (Jerzmańska, 1968; Parin, 1988; Froese & Pauly, 2004).

Genus: †*Kotlarczykia* Jerzmańska, 1974 (MP)

†*Kotlarczykia bathybia* Jerzmańska, 1974, IPM 3 – index species
†*Kotlarczykia* sp. (IPM 3, 5)

Compared to recent representatives (genera: *Margrethia* Jespersen & Taning, 1919 and *Bonapartia* Goode & Bean, 1896), this species probably occurred at depths of 100–700 m (mesopelagic). These are marine fish that dwell continental or insular slopes. Recent related genera are able to migrate vertically throughout the day; they dwell shallower waters at night, migrating deeper during the daylight. Larger specimens prefer deeper waters. They occur in deep-water, subtropical and tropical climates Jerzmańska, 1974, Froese & Pauly, 2004).

Family: STERNOPTYCHIDAE – deep-sea hatchet fishes (MB) (IPM 1, 3, 4A, 4, 5, 6, 7)

Genus: *Polyipnus* Günther, 1887 (MP)

†*Polyipnus* cf. *anteasteroides* Ciobanu, 1977 (IPM 3, 4, 5)

†*Polyipnus brevis* Horbatsch, 1961, IPM 3 – index species

†*Polyipnus sobniovienensis* Jerzmańska, 1960, IPM 4 – index species

†*Polyipnus* cf. *sobniovienensis* Jerzmańska, 1960 (IPM 4)

Polyipnus sp. (IPM 1, 3, 4A, 4, 5, 6)

Depth range: 50–1,023 m (meso-pelagic). Exclusively marine species, bearing photophores. Prefer deep-water climate, but can also be found upon continental slope (Jerzmańska, 1960; Ciobanu, 1977; Parin, 1988; Weitzman, 1997; Froese & Pauly 2004).

Genus: *Argyropelecus* Cocco, 1829 (MB)

†*Argyropelecus cosmovicii* Cosmovici et Paucă, 1943, IPM 6 – index species

Argyropelecus sp. (IPM 5, 6)

Depth range of recent forms: 100–2,960 m (Froese & Pauly, 2004), or 0–4,060 m (Weitzman, 1997). This is a marine, meso- and bathypelagic species, capable of short-term migrations (both adult and juvenile individuals); similarly as representatives of the family Gonostomatidae capable of vertical migrations throughout the day; some individuals come at night closer to the shoreline, at a depth of 100 m (Jerzmańska, 1968; Ciobanu, 1977; Parin, 1988; Froese & Pauly, 2004).

Family: PHOTICHTHYIDAE acc. to Nelson, 1994 (PHOSICHTHYIDAE) lightfishes (MB) (IPM 1, 3, 4, 6, 7)

Genus: *Vinciguerria* Jordan et Evermann, 1896 (MB)

†*Vinciguerria distincta* Daniltschenko, 1962 (IPM 1, 3, 6, 7)

†*Vinciguerria merklini* Daniltschenko, 1946 (IPM 4, 6)

†*Vinciguerria obscura* Daniltschenko, 1946 (IPM 1, 4)

†*Vinciguerria talgiensis* Daniltschenko, 1946 (IPM 1)

Vinciguerria sp. (IPM 1, 3, 4, 5, 6, 7)

Depth range: 20–5,000 m (Froese & Pauly, 2004) or down to 2,000 m (Weitzman, 1997). These are deep-water, meso- and bathypelagic, marine forms, bearing photophores. Both juvenile and adult individuals rest during the daylight in deeper waters (200–600 m); coming to shallower depths at night (0–500 m). They prefer subtropical, deep-water environments (Daniltschenko, 1960, 1980b; Jerzmańska, 1968; Ciobanu, 1977; Parin, 1988).

Order: AULOPIIFORMES (EP, MB) (IPM 2, 4A, 4)

Family: PARALEPIDIDAE – barracudinas (EP, BP) (IPM 2, 4A)

Recent representatives of this family are pelagic or bathypelagic, marine, oceanodromic fish that dwell waters of depths between 0 and 3,000 m, in deep-water climate (Froese & Pauly, 2004).

Genus: †*Holosteus* Agassiz, 1839 (MB)

†*Holosteus mariae* (Menner, 1948) (IPM 2)

†*Holosteus* sp. (IPM 2, 4A, 4)

The present-day genera of this family are exclusively marine, oceanodromic, meso- and bathypelagic fish (preferring deep-water environment), occurring down to a depth of 3,000 m (Daniltschenko, 1960, 1980b; Weitzman, 1997; Froese & Pauly, 2004).

Order: MYCTOPHIFORMES – (BP) (IPM 1, 2, 3, 4A, 4, 5, 6, 7)

Family: MYCTOPHIDAE – lanternfishes (BP) (IPM 1, 2, 3, 4A, 4, 5, 6)

Genus: †*Eomyctophum* Daniltschenko, 1947 (BP)

†*Eomyctophum* cf. *koraense* Daniltschenko, 1947 (IPM 4A, 4, 6, 7)

†*Eomyctophum limicola* Daniltschenko, 1960, IPM 1 – index species

†*Eomyctophum menneri* Daniltschenko, 1947, IPM 7 – index species (IPM 4, 6)

†*Eomyctophum* sp. (IPM 1, 3, 4A, 4, 5, 6, 7)

These marine (bathypelagic, oceanodromic) species occur down to a depth of 1,400 m. They come to the surface at night and remain in near-surface waters to a depth not exceeding 450 m (nyctopelagic); during the daylight they tend to remain at depths between 200 and 900 m (Daniltschenko, 1960, 1980b; Jerzmańska, 1960, 1968; Parin, 1988; Weitzman, 1997; Froese & Pauly 2004).

Genus: *Protomyctophum* Fraser-Brunner, 1949 (BP)

Protomyctophum sp. (IPM 6).

These are marine, bathypelagic, pelagic, oceanodromic fishes, dwelling a depth range of 0 to 1,500 m. They come to the surface at night and remain in near-surface waters down to a depth of 426 m (nycto-epipelagic); preferring deeper waters (600–700 m) during the daylight (Weitzman, 1997; Froese & Pauly, 2004).

Genus: *Diaphus* Eigenmann et Eigenmann, 1890 (BP)

Diaphus sp. (IPM 1).

These are bathypelagic forms that dwell marine waters down to depths exceeding 1,000 m. They tend to migrate vertically throughout the day, similarly as other representatives of this family. Vertical tiering consists in the fact that young and small-size individuals occupy shallower waters, as opposed to adult and larger specimens (Ciobanu, 1977; Weitzman, 1997; Froese & Pauly, 2004).

Order: GADIFORMES (BEP, BD+D, EP, MB, N) (IPM 1, 2, 3, 4A, 6, 7, INM 1)

Family: MORIDAE – morid cods (MB) (IPM 6)

Deep-water fishes (Nelson, 1994)

Family: BREGMACEROTIDAE – codlets (MB) (IPM 3, 4A)

Genus: *Bregmaceros* Thompson, 1840 (MB)

†*Bregmaceros filamentosus* (Priem, 1908), IPM 3 – index species (IPM 4A)

Bregmaceros sp. (IPM 3, 4A)

Depth range: 0–2,000 m (meso- and bathypelagic, as well as some neritic forms). These are marine, tropical and subtropical fish; although brackish and oceanic forms occur as well. They dwell littoral, continental shelf, and open waters. Some of them are capable of migrating vertically, owing to changes in the oxygen content (Daniltshenko, 1960; Parin, 1988; Froese & Pauly, 2004).

Family: PHYCIDAE – phycid hakes (BEP) (IPM 2, 4A, 6)

Genus: †*Eophycis* Jerzmańska, 1968 (BEP)

†*Eophycis jammensis* Jerzmańska, 1968 (IPM 2)

†*Eophycis* sp. (IPM 2)

Depth range: 0–1,400 m (Froese & Pauly, 2004) (benthopelagic). Representatives of the present-day genus *Phycis* do not migrate, and are to be found upon shelf or continental slope. Adult forms prefer the latter environment, while young ones dwell near-shore waters and are able to survive even in river mouths. They occupy either hard or sand-muddy bottom. These are nocturnal forms which hide between rocks during the daylight (Jerzmańska, 1968; Świdnicki, 1990; Świdnicki *et al.*, 1990; Weitzman, 1997).

Genus: †*Onobrosmius* Bogatshov, 1938 (BEP)

†*Onobrosmius* sp. (IPM 4A, 6)

Fishes of this family are benthopelagic fishes and dwell waters of moderate through subtropical and deep-water climate, occurring in both littoral and deep-water basins (50–2,500 m); either solitary or in groups exceeding 100 specimens (Daniltshenko, 1960; Weitzman, 1997; Froese & Pauly, 2004).

Genus: †*Pseudoraniceps* Fedotov, 1974 (D)

†*Pseudoraniceps* sp. (IPM 4A).

This form is comparable to the recent genus *Raniceps*. Recent tadpole cods are demersal, not migrating (or only at short distances) fishes that occur in brackish and marine waters at depths ranging from 0 to 100 m. They usually dwell littoral waters (depths 10–20 m), over a rocky bottom covered with algae (Daniltshenko, 1980b; Parin, 1988; Fedotov & Bannikov, 1989; Świdnicki *et al.*, 1990; Froese & Pauly, 2004).

Family: MERLUCCIIDAE – merluccid hakes (BEP, BD+D) (IPM 1, 2, 3, 4, 5, 6, 7, INM 1)

Genus: †*Palaeogadus* Rath, 1859 (BEP)

†*Palaeogadus abbreviatus* (Bogatshov, 1935) (IPM 2)

†*Palaeogadus carpathicus* Świdnicki, 1991 (IPM 6, 7)

†*Palaeogadus distinctus* Świdnicki, 1990 (IPM 5, 6, 7)

†*Palaeogadus intergerinus* Daniltshenko, 1947 (IPM 6, 7)

†*Palaeogadus simionescui* (Simionescu, 1905), IPM 2 – index species

†*Palaeogadus* sp. (IPM 1, 2, 3, 4, 6)

These fossil, benthopelagic, oceanodromic, brackish or marine fishes used to occur at depths not exceeding 875 m. Similarly to their recent equivalents, they were able to inhabit different environments: from the shoreline to deeper waters on the continental shelf. They probably formed shoals (Daniltshenko, 1960, 1980b; Jerzmańska, 1968; Fedotov & Bannikov, 1989; Weitzman, 1997; Froese & Pauly, 2004).

Genus: *Merluccius* Rafinesque, 1810 – hake (BEP)

†*Merluccius errans* (Smirnov, 1935) INM 1 – index species

†*Merluccius hartensis* Świdnicki, 1990 INM 1-L_{SUB} – index species

Merluccius sp. (IPM 2, 4, 5, 6, 7, INM 1)

Depth range: 50–1,000 m (usually 150–555 m). Hakes are benthopelagic, oceanodromic, marine fishes that dwell either shelf or continental slope. They tend to keep close to the bottom during the daylight, and migrate upwards at night (70–370 m). These fishes are capable of seasonal migrations: towards southern, shallower waters in winter times, and towards northern, deeper waters in summers. They prefer deep-water, moderate through subtropical environments, and usually form shoals (Daniltshenko, 1960, 1980b; Jerzmańska, 1968; Parin, 1988; Weitzman, 1997; Froese & Pauly, 2004).

Genus: †*Parasteindachneria* Świdnicki, 1990 (BD)

†*Parasteindachneria oligocaenica* Świdnicki, 1990 (IPM 6, 7)

Depth range: 400–500 m (bathy-demersal). The present-day genera are marine, deep-water fishes that dwell soft substratum of the outer shelf and upper continental slope. They tend to bear photophores (Świdnicki, 1990; Froese & Pauly, 2004).

Family: GADIDAE – cods (BEP, BD + D) (IPM 1, 2, 3, 6)

Genus: †*Palaeomolva* Daniltshenko, 1947 (BD + D)

†*Palaeomolva monstrata* Fedotov, 1974 (IPM 4, 6)

†*Palaeomolva* sp. (IPM 2, 3, 6)

Recent representatives of genus *Molva* dwell water depths of 30–1,500 m (usually not exceeding 1,000 m) and are demersal, marine fishes. The present-day genera dwell close to the bottom, upon either muddy or hard substratum of the continental slope (Daniltshenko, 1960, 1980b; Fedotov & Bannikov, 1989; Świdnicki, 1990; Weitzman, 1997; Froese & Pauly, 2004).

Order: OPHIDIIFORMES (BEP) (IPM 1, 2, 5, 6, 7)

Family: OPHIDIIDAE (BROTULIDAE) – cusk eels (BEP) (IPM 1, 6, 7)

Genus: †*Propteridium* Arambourg, 1967 (BEP)

†*Propteridium* sp. (IPM 6).

These are probably benthopelagic fishes, whose contemporary representatives inhabit subtropical and tropical waters, not exceeding a depth of 4,000 m (Ciobanu, 1977; Parin, 1988; Świdnicki, 1988; Froese & Pauly, 2004).

Genus: *Glyptophidium* Alcock, 1889 (BEP) (IPM 6, 7)

Glyptophidium sp. (IPM 6, 7).

These are benthopelagic (40–825 m), marine fishes (Świdnicki, 1988a; Froese & Pauly, 2004).

Order: LOPHIIFORMES – anglerfishes (MB, BD + D, EP) (IPM 3, 4A, 5, 6)

Family: ANTENNARIIDAE – frogfishes (BD + D, EP) (IPM 3, 4A, 6)

The representatives of this family dwell all tropical seas down to a depth of 300 m, averaging at some 40 m or less (demersal forms). They occupy reef, marine and brackish waters. Juveniles are benthic forms, except for those of a pelagic genus *Histrio*, which float among *Sargassum* seaweeds (Froese & Pauly, 2004).

Family: CERATIIDAE – seadevils (BP) (IPM 5, 6)

A characteristic feature of these fishes is the presence of a decoy organ (illicium), supplied with photophores. These are marine fishes occurring at great depths, down to 2,090 m (Parin, 1988; Froese & Pauly, 2004).

Order: MUGILIFORMES (N) (IPM 3)

Family: MUGILIDAE – mullets (N) (IPM 3)

These fishes are ubiquitous throughout the seas of tropical

and temperate climate, and include predominantly marine (littoral) and brackish forms, although some species dwell also fresh waters and river mouths (Froese & Pauly, 2004).

Genus: *Mugil* Linnaeus, 1758 (N)
Mugil sp. (IPM 3).

These are cosmopolitan fishes that occur in different marine subtropical and tropical basins. They are represented by benthopelagic, kathadromic, marine, fresh-water, and brackish forms. Their depth range does not exceed 120 m. The species is a littoral one, being frequently spotted in river mouths. These fishes tend to form shoals above sandy, muddy, and densely vegetated bottom, and are active mainly during the daylight (Froese & Pauly, 2004).

Order: BELONIFORMES (EP, R + N) (IPM 2)
Family: HEMIRAMPHIDAE – halfbeaks (R + N, EP) (IPM 2)
Genus: *Hemiramphus* Cuvier, 1817 (R + N)
†*Hemiramphus jerzyi* Jerzmańska, 1968 (IPM 2)

Depth range: 0–5 m; marine forms dwelling reefs and open ocean waters; some recent forms are capable of surviving in brackish waters. These are ocean surface dwellers (Jerzmańska, 1968, 1985; Froese & Pauly, 2004).

Order: BERYCIFORMES (BD + D, BEP, MB, R+N) (IPM 1, 3, 4A, 4, 5, 6, 7)
Family: TRACHICHTHYIDAE – roughies (BP, BEP, R + N) (IPM 4A, 4, 5, 6, 7)

The representatives of this family, typified by a confined body, are bathy- and benthopelagic (10–1,800 m); oceanodromic; marine forms which also dwell reef environments. They prefer deep-water, subtropical to tropical climates; dwell close to the either hard or muddy substratum of continental slope or reefs (Weitzman, 1997; Froese & Pauly, 2004).

Genus: †*Africentrus* (Paučá, 1931) (R + N)
†*Africentrus* sp. (IPM 4A, 4, 5, 6, 7)

The present-day genera are reef, marine dwellers (0–180 m). Most of them display nocturnal activity, hiding among corals and in caves or depressions during the daylight (Froese & Pauly, 2004).

Family: BERYCIDAE – alfonsinos (BD + D, BEP) (IPM 3, 4A, 4, 5, 6)
Genus: †*Paraberyx* Jerzmańska, 1975 (BD + D)
†*Paraberyx bachoviensis* Jerzmańska, 1975 (IPM 6)
†*Paraberyx* sp. (IPM 6)

These are bathydemersal, demersal, benthopelagic, marine fish that dwell a depth interval of 25–1,300 m (usually 200–600 m). Berycids are known from deep-water, subtropical climate, and are to be found shortly above sandy and muddy substratum situated off the shelf, above continental slope. Adult specimens are demersal forms, while the juveniles ones – pelagic ones. Some of them migrate at night towards more shallower waters (Jerzmańska & Kotlarczyk, 1975; Weitzman, 1997; Froese & Pauly, 2004).

Family: HOLOCENTRIDAE – squirrelfishes (R + N, BD + D) (IPM 4A, 4, 5, 6, 7)
Genus: †*Holocentroides* Paučá, 1931 (R + N)
†*Holocentroides moldavicus* Paučá, 1931 (R + N) (IPM 4, 6, 7)
†*Holocentroides* sp. (IPM 4A, 4, 5, 6)

Recent representatives of this family from genera *Holocentrus*, *Sargocentron*, and *Myripristis* dwell mostly reef, marine environments (0–180 m). Most of them show nocturnal activity, hiding during the daylight among corals and within caves or de-

pressions. Some of them tend to cluster into small groups. Adult specimens represent demersal forms (Bannikov & Parin, 1997; Froese & Pauly, 2004).

Order: ZEIFORMES (BEP, BD + D, R + N) (IPM 1, 2, 3, 4A, 4, 6)
Family: ZEIDAE – dories (BEP) (IPM 1, 3, 4A, 4, 6)
Genus: *Zenopsis* Gill, 1862 (BEP)
†*Zenopsis clarus* Daniltshenko, 1960 (IPM 1, 3)
Zenopsis sp. (IPM 3, 4A)

These are benthopelagic (30–800 m; usually 90–360 m), marine, deep-water fish that occur either close to the bottom, or within water column, or upon muddy substratum. Some forms can also be found in deeper parts of the shelf and continental slope (Daniltshenko, 1960, 1980; Świdnicki, 1986; Froese & Pauly, 2004).

Genus: *Zeus* Linnaeus, 1758 (BEP)
Zeus faber Linnaeus, 1758 (IPM 4A, 4, 6)
Zeus sp. (IPM 3, 4A, 5, 6)

These are benthopelagic (5–400 m), oceanodromic, marine fishes that dwell temperate climate waters, and dwell near the sandy or muddy bottom (Świdnicki, 1986; Froese & Pauly, 2004).

Order: CAPROIFORMES (R + N, BD + D) (IPM 1, 2, 4A, 6)
Family: CAPROIDAE – boarfishes (BD + D, R + N) (IPM 1, 2, 4A, 6)
Genus: *Antigonia* Lowe, 1843 (BD + D)

Antigonia sp. (IPM 4A, 6). This genus is represented by demersal, marine forms that occur in a depth interval of 50 to 900 m, within subtropical, tropical, deep-water environments. They dwell close to the bottom on either shelf or continental slope. Juveniles tend to occur in the water column (Świdnicki, 1986, 1988b; Froese & Pauly, 2004).

Genus: *Capros* Lacépède, 1802 (BD + D, R + N)
†*Capros medianus* Świdnicki, 1986 (IPM 6)
†*Capros radobojanus* (Kramberger, 1882) (IPM 1, 2, 4A, 6)
Capros sp. (IPM 2, 4A)

These are demersal (40–600 m), marine fishes of subtropical climate which form shoals in a reef environment. They also occur close to either sandy or rocky bottom (Jerzmańska, 1968; Świdnicki, 1986; Parin, 1988; Froese & Pauly, 2004).

Order: GASTEROSTEIFORMES (EP, BEP, R + N, BD + D) (IPM 1, 2, 3, 4A, 4, 5, 6, 7, INM 1)
Family: AULORHYNCHIDAE – tube-snouts (BEP) (IPM 4A, 6)
These benthopelagic, marine fishes, dwelling waters down to a depth of 30 m, recently occur in different littoral waters of the northern Pacific. They tend to form shoals close to the sea surface (Froese & Pauly, 2004).

Family: SOLENOSTOMIDAE – ghost pipefishes (EP, R + N) (IPM 3)
Genus: †*Solenorhynchus* Heckel, 1854 (EP, R + N)
†*Solenorhynchus* sp. (IPM 3)

Recent representatives of this family dwell tropical marine waters. These are epipelagic, reefal fish which occur down to a depth of 95 m, and close to hard or muddy bottom where they frequently hide between corals, algal mats, or crinoids (Froese & Pauly, 2004).

Family: SYNGNATHIDAE – pipefishes and seahorses (EP, N) (IPM 1, 2, 3, 4A, 4, 5, 6, 7, INM 1)

Genus: *Syngnathus* Linnaeus, 1758 (EP)

†*Syngnathus incompletus* Cosmovici, 1887 (IPM 2, 4, 6, 7), IPM 6-S_{SUB} – index species

Syngnathus sp. (IPM 1, 2, 3, 4A, 4, 5, 6, 7, INM 1)

Syngnathus - typus A (IPM 4A, 5, 6)

Syngnathus - typus B (IPM 5)

Depth range: 0–300 m (epi-pelagial). These are predominantly marine forms; although some specimens are to be found in brackish waters or in river mouths. They dwell in differentiated waters of temperate, subtropical, and tropical climate. Recent representatives tend to occur in littoral waters of either sandy or muddy bottom, usually among algae (*Sargassum*) and seaweeds (*Zostera* and *Posidonia*), which serve as their camouflage (Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1968, 1975; Ciobanu, 1977; Froese & Pauly, 2004).

Genus: †*Hipposyngnathus* Daniltshenko, 1960 (EP, N)

†*Hipposyngnathus neriticus* Jerzmańska, 1968 (IPM 2)

This is an epipelagic (0–100 m), marine species. Some forms are brackish or dwell in river mouths. Prefer waters of temperate, subtropical, and tropical climate. Recent genera dwell in littoral waters of sandy or muddy bottom, occurring among algae (*Sargassum*) and seaweeds (*Zostera* and *Posidonia*), which serve as their camouflage (Daniltshenko, 1960, 1980b; Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1968; Froese & Pauly, 2004).

Family: AULOSTOMIDAE – trumpetfishes (R + N) (IPM 4A)

These fish occur in tropical seas, within reef environments of the Atlantic and Indo-Pacific, at depths ranging between 3 and 122 m (Froese & Pauly, 2004).

Family: FISTULARIIDAE – cornetfishes (EP, R + N, D) (IPM 2, 3, 4A, 7)

The fistularids are marine, tropical and subtropical, epipelagic, reef, and demersal (0–200 m) fishes. They occur on continental, reef, and insular margins, except for places of intense wave action, and dwell in sandy, muddy or hard bottom covered with vegetation (Froese & Pauly, 2004).

Genus: *Fistularia* Linnaeus, 1758

Fistularia sp. (IPM 2, 4A, 7).

The representatives of this genus are characteristic of epipelagic and reef environments (depth range: 0–200 m) of both marine and brackish waters of tropical climate. They occur either solitary or in shoals, among reefs and algae, as well as at a soft bottom, feeding on fish, small crustaceans, and cephalopods (Froese & Pauly, 2004).

Family: CENTRISCIDAE – shrimpfishes (R + N, EP) (IPM 1, 4A, 6)

Genus: *Centriscus* Linnaeus, 1758 (R + N, EP)

†*Centriscus heinrichi* (Heckel, 1850), IPM 1-C_{SUB} – index species

†*Centriscus longispinus* Rozhddestvenski, 1949, IPM 1-C_{SUB} – index species

†*Centriscus teleajensis* Jonet, 1949 IPM 1-C_{SUB} – index species

†*Centriscus* nov.sp. IPM 4A – index species

Centriscus sp. (IPM 1, 4A, 6)

These are reefal, neritic, epipelagic (3–100 m), and also demersal marine forms. Some individuals can also occur in brackish waters. They dwell shallow, warm tropical waters, within seagrass, seaweeds, corals, and sea anemones, hiding in rocky fissures

and caves (Daniltshenko, 1960, 1980b; Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1968; Froese & Pauly, 2004).

Order: SCORPAENIFORMES (R + N, BD + D) (IPM 1, 2, 3, 4A, 4, 5, 6, 7)

Family: SCORPAENIDAE – scorpionfishes (R + N, BD + D) (IPM 1, 2, 3, 4A, 4, 5, 6, 7)

Genus: *Scorpaenoides* Priem, 1899 (D, R + N)

†*Scorpaenoides popovicii* Priem, 1899 (IPM 1)

Scorpaenoides sp. (IPM 1, 3, 4A, 4, 5, 6, 7)

Recent demersal, reefal, marine forms occur at depths ranging between 0 and 200 m in temperate through tropical climates. They tend to occur in reef environments, on rocky substratum, close to the bottom; and frequently hide among rubble in caves or fissures, usually near the reef edge. They possess venomous spines (Parin, 1988; Froese & Pauly, 2004).

Genus: *Scorpaena* Linnaeus, 1758 (R + N, BD + D)

Scorpaena sp. (IPM 4A)

These fishes dwell reefal, demersal, marine environment down to a depth of 800 m. They prefer either hard, or muddy and sandy substratum, and dwell among seaweeds in tropical and subtropical seas. They tend to bear spines with venom glands (Parin, 1988; Froese & Pauly, 2004).

Order: PERCIFORMES (EP, MB, D) (IPM 1, 2, 3, 4A, 4, 5, 6, 7, INM 1)

Family: SERRANIDAE – sea basses (BD + D, R + N) (IPM 1, 2, 3, 4A, 4, 5, 6, 7)

Genus: †*Properca* Sauvage, 1880 (R + N)

†*Properca sabbai* Paucă, 1929 (IPM 2, 6)

†*Properca* sp. (IPM 2, 3)

This fossil species is related to the recent representatives of family Serranidae which occur at depths ranging from 0 to 500 m, and are reefal, demersal, marine forms. Some of them are capable of surviving in brackish waters. They prefer subtropical to tropical, deep-water climate (Jerzmańska, 1968; Froese & Pauly, 2004).

Genus: *Serranus* Cuvier, 1817 (BD + D, R + N)

†*Serranus budensis* (Heckel, 1856) (IPM 2, 6)

Serranus sp. (IPM 1, 2, 3, 4A, 4, 5, 6, 7)

Depth range: 0–500 m (demersal, reefal); marine forms. Some forms are capable of surviving in brackish waters. They prefer subtropical to tropical, deep-water climate; dwelling on either rocky, semi-hard, or sandy and muddy substratum, frequently among seaweeds. They spend their spawning season in open waters of the pelagic zone (Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1968; Froese & Pauly, 2004)

Family: PERCIDAE – perches (EP, MB, BEP, D) (IPM 2, 3, 6)

The occurrence of these fish is restricted to the temperate zone of the Northern Hemisphere. Most of them dwell in fresh or brackish waters, down to a depth of 60 m. These are pelagic, benthopelagic, and demersal forms (Froese & Pauly, 2004).

Genus: †*Propercarina* Paucă, 1929 (BEP)

†*Propercarina* sp. (IPM 2, 3, 6).

Recent perches dwell in brackish and fresh waters of temperate climate, down to a depth of 60 m. Genus *Propercarina* is considered as a probably benthopelagic form (Froese & Pauly, 2004).

Family: PRIACANTHIDAE – bigeyes (R + N) (IPM 3, 4, 6)

Genus: *Priacanthus* Oken, 1817 (R + N)

†*Priacanthus longispinus* Lednev, 1914 (IPM 4)

Priacanthus sp. (IPM 3, 4, 5, 6)

Depth range: 10–400 m (reefal, demersal, marine forms).

They are associated with coral reefs and rocky formations of subtropical and tropical climate (Daniltshenko, 1960, 1980b; Jerzmańska & Jucha, 1963; Froese & Pauly, 2004).

Family: APOGONIDAE – cardinalfishes (R + N) (IPM 3, 4A, 6)

Cardinalfishes are mostly marine dwellers that prefer reefs, mangrove forests, and bays covered with seaweeds; some forms occur in brackish and fluvial waters. They prefer a depth range of 0–100 m (Froese & Pauly, 2004).

Family: ECHENEIDAE – remoras (EP) (IPM 2, 4, 5, 6, 7)

Genus: *Echeneis* Linnaeus, 1758 (EP)

†*Echeneis carpathica* Szajnoch, 1926 (IPM 2, 4, 5, 6, 7).

Remoras occur at depths ranging from 20 to 50 m (epipelagic, reefal forms) or 0–100 m (marine forms), in subtropical and tropical waters. They can frequently be found in hot waters near the shore, although being more numerous farther seaward. They also occur around coral reefs. They tend to cling to different host organisms, like sharks, rays, large teleosts, sea turtles or cetaceans, and travel at large distances together with their hosts. They feed on small fish, remains, and skin parasites of their host organisms. Juveniles are resident cleaners of coral reefs. The remoras' spawning season is a pelagic one (Jerzmańska & Świdnicka, 2003; Froese & Pauly, 2004).

Family: CARANGIDAE – jacks and pompanos (EP, BEP, R + N) (IPM 1, 2, 4, 6, INM 1)

Genus: *Caranx* Lacépède, 1802 (R + N, EP)

†*Caranx petrodavae* Simionescu, 1905 (IPM 1, 2, 5, 6)

†*Caranx gracilis* Kramberger, 1882, INM 1 – index species
Caranx sp. (IPM 2, 6)

These fishes occur at present at depths ranging from 0 to 350 m, and represent reefal, epipelagic, and also benthopelagic forms; some of them can survive in brackish waters. They are known from subtropical and tropical seas. These are quickly swimming predators that dwell both coral reefs and open marine waters. They spend their spawning season in littoral waters. Juveniles coexist with seaweeds (*Sargassum*) and jelly fishes. Young individuals penetrate river mouths (Froese & Pauly, 2004).

Genus: †*Archaeus* Agassiz, 1844 (EP)

†*Archaeus* sp. (IPM 6)

A fossil genus related to representatives of genus *Caranx*, occurring at depths between 0 and 350 m. The present-day forms are epipelagic, benthopelagic, and marine ones; some of them can also be found in brackish waters. They tend to occur in subtropical and tropical climate, both near coral reefs and in open sea; usually solitary, occasionally forming shoals (during the daylight) or small groups. Juveniles frequently coexist with seaweeds (*Sargassum*) and jelly fish (Jerzmańska & Kotlarczyk, 1975; Bannikov, 1990; Froese & Pauly, 2004)

Family: LEIOGNATHIDAE – ponyfishes (BEP, D) (IPM 2, 4, INM 1)

Genus: *Leiognathus* Lacépède, 1803 (BEP, D)

†*Leiognathus* cf. *minutus* Daniltshenko, 1980 INM 1-L.SUB. – index species

Leiognathus sp. (IPM 2, 4)

Genus: *Equula* Cuvier, 1815 (BEP, D)

Equula? sp. (IPM 4)

Depth range: 10–110 m (benthopelagic, demersal forms). These are marine and brackish fishes; some forms are able to penetrate fresh waters where they occur close to the shore and in tidal bays, usually of muddy bottoms. They bear photophores (Jerzmańska, 1960; Daniltshenko, 1980b; Nelson, 1994; Jerzmańska *et al.*, 2001; Froese & Pauly, 2004).

Family: CHAETODONTIDAE – butterflyfishes (R + N) (IPM 4A)

The fishes of this family presently occur in the Atlantic, Indian and Pacific oceans, within temperate through tropical waters, mostly in reefal environments. They spend their spawning season in the pelagial zone (Froese & Pauly, 2004).

Genus: *Forcipiger* Jordan et Mc Gregor, 1898 (R + N)

Forcipiger sp. (IPM 4A).

These are small, up to 22 cm long, tropical, reefal, not migrating, exclusively marine fishes which do not exceed 100 m depth. They tend to occur in reefs and lagoons (Froese & Pauly, 2004).

Family: AMMODYTIDAE – sand lances (BEP) (IPM 1, 2, 6)

Genus: *Ammodytes* Linnaeus, 1758 (BEP)

†*Ammodytes antipai* Paucă, 1929 (IPM 1, 2)

Ammodytes sp. (IPM 2, 6)

Recent sand lances occur at depths between 0 and 100 m, representing benthopelagic, demersal, marine, and brackish forms that tolerate arctic through temperate climates. They include either territorial forms, or those occurring in shoals near the coastline, penetrating river mouths, bays, and beaches. They drill sand looking for food (Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1968; Froese & Pauly, 2004).

Family: TRACHINIDAE – weeverfishes (D) (IPM 2)

Genus: *Trachinus* Linnaeus, 1758 (D)

†*Trachinus minutus* (Jonet, 1958) IPM 2-T.SUB. – index species

Trachinus sp. (IPM 2)

Depth range: 0–150 m (demersal; marine forms). They occupy waters of temperate through subtropical climate. Weeverfishes dwell shallow waters close to the bottom, drilling the substratum. At night, they tend to swim slowly in pelagial waters. These fish bear venomous spines (Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1968; Froese & Pauly, 2004).

Family: GOBIIDAE – gobies (D) (INM 1)

Genus: *Gobius* Linnaeus, 1758 (D)

Gobius sp. (INM 1).

These fishes occur at depths between 0 and 80 m, being represented by demersal, mostly marine forms, although some species are brackish and also kathadromic. They are to be found in subtropical and tropical climate, occurring frequently in fresh-water and brackish basins on oceanic islands, and also in reef environments, within seaweeds, where they hide close to the bottom, commonly among rock rubble (Jerzmańska *et al.*, 2001; Froese & Pauly, 2004).

Family: ACANTHURIDAE – surgeonfishes (R + N, BEP) (IPM 4A)

Genus: †*Caprovesposus* Daniltshenko, 1960 (BEP)

†*Caprovesposus* sp. (IPM 4A)

Recent representatives of this family are tropical fishes occurring at depths of 0 to 90 m. These are benthopelagic, reefal, marine organisms which co-exist with *Sargassum* and *Dictyota* seaweeds. They feed on algae, zooplankton and detritus, and reproduce in pelagial waters (Daniltshenko, 1960, 1980b; Froese & Pauly, 2004).

Family: SPHYRAENIDAE – barracudas (EP, R + N) (IPM 5)

These predatory subtropical and tropical fishes occur throughout the world ocean, and are represented by pelagic and reefal forms that are to be found at depths of 0 to 100 m. They spend their

spawning season in shoals in pelagial waters (Froese & Pauly, 2004).

Genus: *Sphyraena* Röse, 1793 (EP)
Sphyraena sp. (IPM 5).

This genus includes fishes occurring at depths not exceeding 100 m, although usually close to the surface, both in open ocean and in reefs. Juveniles can be found in mangroves, estuaries, and bays. These are marine, brackish, subtropical forms (Froese & Pauly, 2004).

Family: †EUZAPHLEGIDAE (EP) (IPM 1, 2)
Genus: †*Palimphytes* Agassiz, 1844 (EP)
†*Palimphytes lanceolata* Simionescu, 1905 (IPM 1)
†*Palimphytes* sp. (IPM 1, 2)

This fossil genus is considered to be related to recent representatives of genus *Scomber*, which are associated with pelagial zone (0–300 m), and include oceanodromic fishes that occur in temperate and subtropical waters and are capable of large-scale migrations. They tend to form large shoals together with similar-shaped specimens of their family, as well as Clupeiformes. These fishes cluster below the surface during the daylight and migrate into open waters at night (Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1968; Parin, 1988; Froese & Pauly, 2004).

Family: GEMPYLIDAE – snake mackerels (BEP) (IPM 1, 3, 4A, 4, 5, 6, 7)

Genus: †*Hemithyrsites* Sauvage, 1873 (BEP)
†*Hemithyrsites rumanus* (Jonet, 1958) (IPM 3, 6)
†*Hemithyrsites* sp. (IPM 3, 4A, 4, 5, 6, 7)

These are benthopelagic, marine fish occurring at depths of 0 to 400 m in subtropical, deep-water climate. Recent genera tend to come close to the surface at night. They dwell on slopes of submarine mounts and ridges (Parin, 1988; Weitzman, 1997; Froese & Pauly, 2004).

Genus: *Thyrstitoides* Fowler, 1929 (BEP)
†*Thyrstitoides* sp. (IPM 1, 3, 4A, 4, 6, 7)

These are exclusively marine, benthopelagic, deep-water fishes occurring at depths of 0 to 400 m. They tend to come close to the surface at night, and dwell on slopes of submarine mounts and ridges (Parin, 1988; Weitzman, 1997; Froese & Pauly, 2004).

Family: TRICHIURIDAE – cutlassfishes (BEP, BD) (IPM 1, 2, 3, 4A, 4, 5, 6, 7, INM 1)

Genus: *Lepidopus* Gouan, 1770 (BEP)
†*Lepidopus glarisanus* (Blainville, 1818) (IPM 1, 2, 6)
†*Lepidopus isopleurus* (Agassiz, 1843) (IPM 3, 6, 7)
Lepidopus sp. (IPM 1, 2, 3, 4A, 4, 5, 6, 7, INM 1)

Depth range: 20–500 m (usually 200–400 m). These are benthopelagic, bathy-demersal fishes that occur in subtropical and tropical, deep-water climate. Juveniles prefer pelagic waters. They are to be found on continental shelf, close to its edge and upper part of slope; sometimes close to sandy and muddy bottom. At night, they tend to migrate into open waters (Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1968; Ciobanu, 1977; Parin, 1988; Froese & Pauly, 2004).

Family: †PALAEORHYNCHIDAE (EP)
(IPM 1, 2, 3, 4A, 4, 5, 6)

Genus: †*Palaerhynchus* Blainville, 1818 (EP)
†*Palaerhynchus* sp. (IPM 1, 2, 3, 4A, 4, 5, 6)

This fossil family, belonging to suborder Scombroidei, included epipelagic forms (0–200 m) (Daniltshenko, 1960, 1980b; Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1968; Froese & Pauly, 2004).

Family: SCOMBRIDAE – mackerels and tunas (EP) (IPM 1, 2, 3, 4A, 4, 5, 6, 7)

Genus: *Scomber* Linnaeus, 1758 (EP)
†*Scomber voitestii* Pauca, 1929 (IPM 2, 4A, 4, 5, 6).

Recent mackerels occur at depths ranging between 0 and 300 m, and represent pelagic, oceanodromic, marine and brackish forms dwelling in temperate and subtropical waters. They are capable of large-scale migrations; tend to form large shoals together with similar-sized specimens of their family, as well as Clupeiformes. They swim below the surface during the daylight and migrate into open waters at night (Jerzmańska, 1968; Jerzmańska & Kotlarczyk, 1975; Bannikov, 1985a; Parin, 1988; Froese & Pauly, 2004).

Genus: *Acanthocybium* Gill, 1862 (EP)
Acanthocybium sp. (IPM 5, 6).

This is an oceanic, oceanodromic, epipelagic fish which occurs in tropical climate at depths not exceeding 12 m, either solitary or in small groups (Parin, 1988; Froese & Pauly, 2004).

Genus: *Sarda* Cuvier, 1829 (EP, N)
Sarda sp. (IPM 2, 4, 5).

These are epipelagic, neritic, oceanodromic, marine fishes (0–200 m), known from subtropical waters. They form large shoals, and are capable of penetrating river mouths. Some of them are littoral forms (Jerzmańska, 1960; Parin, 1988; Froese & Pauly, 2004).

Family: NOMEIDAE – driftfishes (EP, MB, D) (IPM 4A, 5, 6)
Genus: †*Psenicubiceps* Daniltshenko, 1980 (MP)
†*Psenicubiceps* sp. (IPM 4A, 5, 6)

Driftfishes are subtropical and tropical, mesopelagic and demersal (both brackish and marine) forms that occur at depths ranging between 50 and 1,000 m. They are accompanied by jelly fishes, drifting vegetation, and *Sargassum* algae. Juveniles are pelagic forms, while larger specimens occur close to the bottom and on continental slope. They can migrate to the surface at night (Daniltshenko, 1980b; Weitzman, 1997; Froese & Pauly 2004).

Family: STROMATEIDAE – butterfishes (BEP) (IPM 2, 5, 6)
Genus: †*Pinichthys* Bannikov, 1985 (BEP)
†*Pinichthys* sp. (IPM 2, 5, 6)

These are subtropical and tropical fishes occurring close to the coastline. Recent representatives of butterfishes are benthopelagic (0–110 m) forms of both marine and brackish waters. They occur on continental shelf in summer, migrating farther seaward in winter. They tend to form shoals, are frequently accompanied by representatives of genera *Leiognathus* and *Nemipterus*, as well as jelly fishes and drifting vegetation (young forms), swimming above muddy and sandy bottom (Froese & Pauly, 2004).

Order: PLEURONECTIFORMES (BD + D)
(IPM 1, 2, 4A, 4, 5, 6)

These demersal, brackish, fresh-water, kathadromic, and marine forms of confined bodies occur at depths of 0–1,000 m. They usually occur close to the bottom. Their eyes are located on the right side of the body. These fishes are capable of changing colour, depending on the substratum. They occur upon either sandy, or muddy or gravelly bottom, and spend their spawning season in pelagic waters (Jerzmańska & Kotlarczyk, 1988; Froese & Pauly, 2004).

Family: PSETTODIDAE – psettodids (BD + D) (IPM 4)

The representatives of this family are demersal, marine, and brackish forms known from tropical waters of Western Africa and

the Indo-Pacific. They occur at depths not exceeding 150 m, upon both sandy and muddy bottom (Froese & Pauly, 2004).

Order: TETRAODONTIFORMES (BP + D, BP, R + N)
(IPM 1, 3, 4A, 5, 6)

Family: TRIACANTHODIDAE – spikefishes (BP + D)
(IPM 4A, 6)

Genus: †*Carpathospinosus* Tyler et Jerzmańska, Bannikov, Świdnicki, 1993 (BD + D)

†*Carpathospinosus propheticus* Tyler et Jerzmańska, Bannikov, Świdnicki, 1993, IPM 4A – index species
†*Carpathospinosus* sp. (IPM 4A)

This fossil genus is related to the recent genera *Triacanthodes* Bleeker, 1858, *Bathyphylax* Myers, 1934, *Mephisto* Tyler, 1934 and *Paratriacanthodes* Fowler, 1934, which occur at depths of 50–615 m in the tropics. These were demersal, bathy-demersal, marine fishes occurring on the shelf and its edge, close to the sandy and muddy bottom (Tyler *et al.*, 1993; Santini & Tyler, 2003; Froese & Pauly, 2004).

Genus: †*Prohollandia* Tyler et Jerzmańska, Bannikov, Świdnicki, 1993 (BP)

†*Prohollandia avita* Tyler et Jerzmańska, Bannikov, Świdnicki, 1993 (IPM 6)

Recent, related genera occur at depths of 100–400 m (*Parahollandia* Fraser-Brunner 1941) and 50–915 m (*Hollandia* Poey, 1861). The fossil genera were probably represented by bathypelagic, exclusively marine forms which occurred in subtropical and tropical, deep-water climate. They could have dwelled deeper parts of coral reefs (Tyler *et al.*, 1993; Santini & Tyler, 2003; Froese & Pauly, 2004).

Genus: *Parahollandia* (Fraser-Brunner, 1941) (BD + D)
Parahollandia sp. (IPM 4A, 6).

This subtropical, demersal fish occurs at depths of 120–400 m, close to the bottom (Froese & Pauly, 2004).

Family: BALISTIDAE – triggerfishes (R + N, EP)
(IPM 3, 4A, 4, 5, 6)

Genus: †*Oligobalistes* Daniltshenko, 1960 (R + N)
†*Oligobalistes* sp. (IPM 4A)

Genus: †*Apostasis* Kramerberger, 1891 (R + N)
†*Apostasis* sp. (IPM 3, 4, 5, 6)

Recent forms occur in subtropical and tropical reefs of the Atlantic, Indian, and Pacific oceans, usually at depths ranging between 0 and 100 m (pelagic waters). They have a compressed body, equipped with first spine in dorsal fin with a closing mechanism. The eyes are located in characteristic box-like sockets which are capable of independent movements. The tail fin is used at quick, short movements (Daniltshenko, 1960, 1980b; Froese & Pauly, 2004).

Family: OSTRACIIDAE – boxfishes (R + N) (IPM 4, 6)

Genus: †*Oligolactoria* Tyler et Gregorová, 1991 (R + N)

†*Oligolactoria bubiki* Tyler et Gregorová, 1991 (IPM 4).

Their trapezoidal-shaped body is covered by a bone armour, except for the core of tail fin. These fishes bear characteristic, cornet-shaped spines above their eyes. At present, they occur in tropical and subtropical seas, in littoral waters, estuaries, and reefs, at depths ranging between 0 and 110 m. Young forms prefer pelagic environment. Some of them are poisonous (Tyler & Gregorová, 1991; Gregorová, 1997; Froese & Pauly, 2004).

Palaeoecology of fish assemblages within ichthyofaunal zones

Palaeoecological interpretation, concerning both environment and bathymetry, is based on qualitative and quantitative analysis of fish specimens included in the distinguished ichthyofaunal zones. Palaeobathymetry of fish genera and their proportions at different depths in each zone are illustrated by bar diagrams, while palaeoecology of respective assemblages is portrayed on circular diagrams. Bathymetric diagrams were compiled basing on the Nolf & Brzobohaty's (1994) method.

Zone IPM 1

The ichthyofaunal assemblage of Zone IPM 1 (Fig. 21) contains nearly 48% of fish dwelling below a depth of 200 m, including index taxa: *Eomyctophum limicola* and *Scopeioides glarisianus*. These include numerous taxa capable of surviving at great depths and bearing photophores (*Scopeioides*, *Polyipnus*, *Vinciguerria*, *Eomyctophum*, *Diaphus*), and those capable of vertical migrations depending on the time of the day (e.g. *Polyipnus*, *Vinciguerria*). Apart from deep-water taxa, the representatives of shallow-water ones occur as well (*Clupea*, *Alosa*, *Syngnathus*, *Palimphytes*, *Palaeorhynchus*, *Cetorhinus*), constituting ca. 29% of the total. Nearly 16.6% comprise benthopelagic fish (*Ammodytes*, *Glossanodon*, *Lepidopus*, *Palaeogadus*, *Thyrstitoides*, *Zenopsis*), while reefal and littoral forms, including subzone index taxa of *Centriscus heinrichi*, *Centriscus longispinus* and *Centriscus teleajensis* make up to 5.9%. The share of fishes associated with the sea bottom, like genera *Capros*, *Scorpaenoides*, *Serranus*, is insignificant (0.3%). The taxa preferring both warm waters, presently occurring in tropical (e.g. *Centriscus*, *Caranx*, *Serranus*, *Capros*) and subtropical seas (*Thyrstitoides*, *Lepidopus*), and those of colder waters (*Ammodytes*, *Palaeogadus*, *Cetorhinus*) are present within the assemblage. The results of palaeoecological and palaeobathymetric analyses point to an open, relatively deep, and very warm basin.

Zone IPM 2

Compared to Zone IPM 1, the Menilite basin contains (see Fig. 22) a surprisingly small number of deep-water taxa (2%), including genus *Holosteus*, while shallow-water representatives are quite frequent (24%). Apart from shallow-water taxa known from Zone IPM 1, there occur new taxa, like: *Fistularia*, *Hipposyngnathus*, *Pomolobus*, *Sarda*, and *Scomber*. The most numerous are fish dwelling close to the bottom, although at small depths (37.9%), including such new taxa, as: *Eophycis*, *Merluccius*, *Propercarina*, *Leiognathus*, and *Pinichthys* (together with the index species of this zone, namely *Glossanodon musceli* and *Palaeogadus simionescui*). Reefal and neritic taxa comprise 2.7% of the assemblage, including new taxa: *Hemiramphus* and *Properca*. The share of fish dwelling near sea bottom increases to 33.4%, being represented by *Capros* and new taxa, like: *Palaeomolva*, *Serranus*, and *Trachinus*. This assemblage suggests a shallowing of the basin. Similarly to Zone IPM 1, there occur forms associated with both tropical and subtropical (*Hemiramphus*, *Pinichthys*, *Leiognathus*,

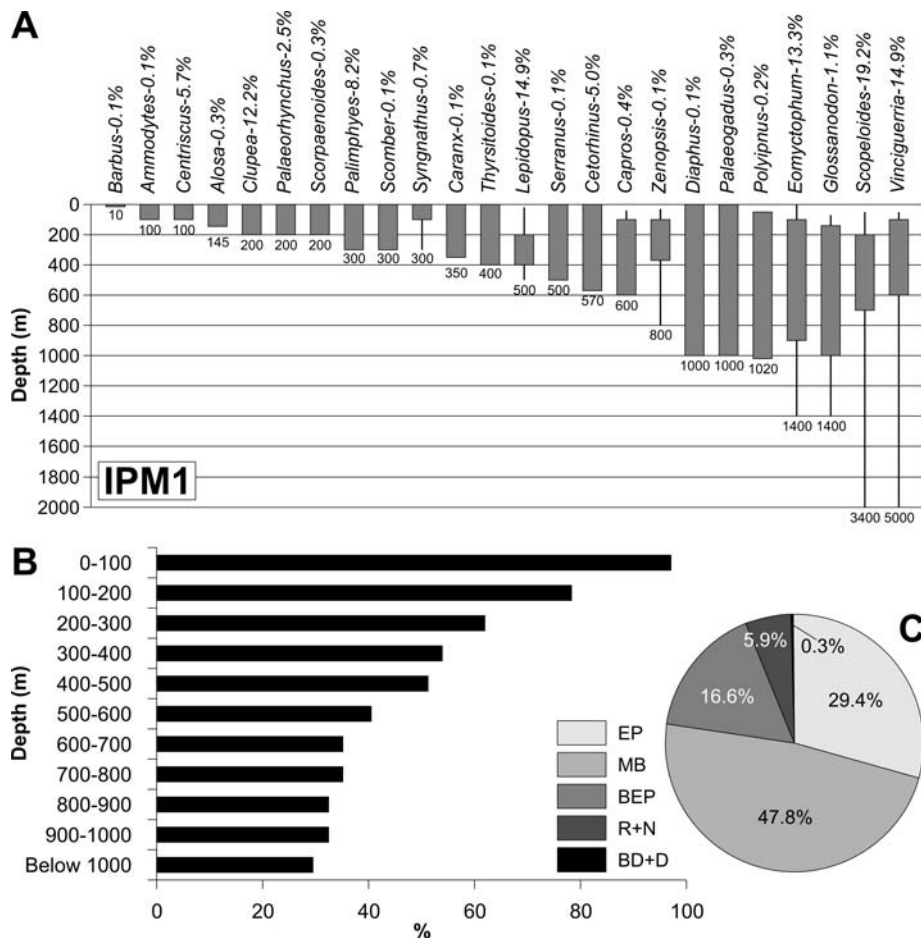


Fig. 21. Palaeobathymetry and palaeoecology of the IPM1 Zone fish assemblage: A – depth intervals of fish genera and share of the latter in the zone's assemblage (including specimens connected with mass mortality events); B – percentage of fish genera of the zone's assemblage occurring at different depths; C – percentage of ecological groups distinguished in the zone (EP – epipelagic, MB – meso-bathypelagic, BEP – bathypelagic, BD+D – bathydemersal and demersal, R+N – reef and neritic)

Fistularia, *Properca*), and temperate and cold climate (e.g. *Propercarina*).

Zone IPM 3

Zone IPM 3 (Fig. 23) marks again the occurrence of more numerous deep-water forms (54.4%). There appear for the first time such taxa, as: *Idrissia*, *Bathypriion*, and *Kotlarczykia*, including index species *Kotlarczykia bathybia*; *Bregmaceros*, together with index species *Bregmaceros filamentosus*; and *Polyipnus*, bearing index species *Polyipnus brevis*. Genus *Solenorhynchus* appears among shallow-water fishes that constitute ca. 18% of the assemblage. Benthopelagic fish are relatively numerous (21.7%), including mostly *Lepidopus*, as well as new genera: *Mugil*, *Zeus*, and *Hemithysites*. The amount of reef taxa, including new genera *Priacanthus* and *Apostasis*, diminishes to 1.1%. Taxa dwelling close to the bottom comprise 5.1% (*Palaeomolva*, *Scorpaenoides*, *Serranus*) of the assemblage. The results of palaeoecological analysis enable one to conclude about the presence of a deep-water basin. The assemblage is dominated by subtropical and tropical forms.

Zone IPM 4A

This zone (Fig. 24) contains numerous shallow-water taxa (27.3%). Benthopelagic fishes amount to 14.6%. In

this group, the genera *Onobrosmius* and *Caprovesposus* appear for the first time. Deep-water forms are scarce (5.9%), including a new genus *Psenicubiceps*. Among fishes typical of reefal environment, there appear new taxa: *Africentrum*, *Forcipiger*, *Holocentroides*, *Oligobalistes*, and *Scorpaena*, with dominating *Centriscus* which makes up ca. 45% of the assemblage. The taxa dwelling close to the bottom, including new genera *Antigonina*, *Pseudoraniceps* and *Parahollandia*, as well as *Carpathospinosus* comprise 7.6%. Most of the taxa characteristic of this zone represent forms whose recent relatives occur in tropical and subtropical climate (e.g. *Caprovesposus*, *Centriscus*, *Fistularia*, *Africentrum*, *Holocentroides*, and others). This assemblage points to the presence of a warm water basin which was shallower as compared to that of Zone IPM 3.

Zone IPM 4

The dominant assemblage (65.6%) of this zone (Fig. 25) comprises deep-water fish, including an index species *Polyipnus sobnioviensis*. Genus *Alopecias* appears for the first time among shallow-water taxa, comprising 18.8% of the assemblage, while genus *Equula* appears for the first time among benthopelagic taxa (8.1%). Infrequent reef-neritic fish (5.7%) include species *Oligolactoria bubiki* and *Priacanthus longispinus*, which are known from this zone

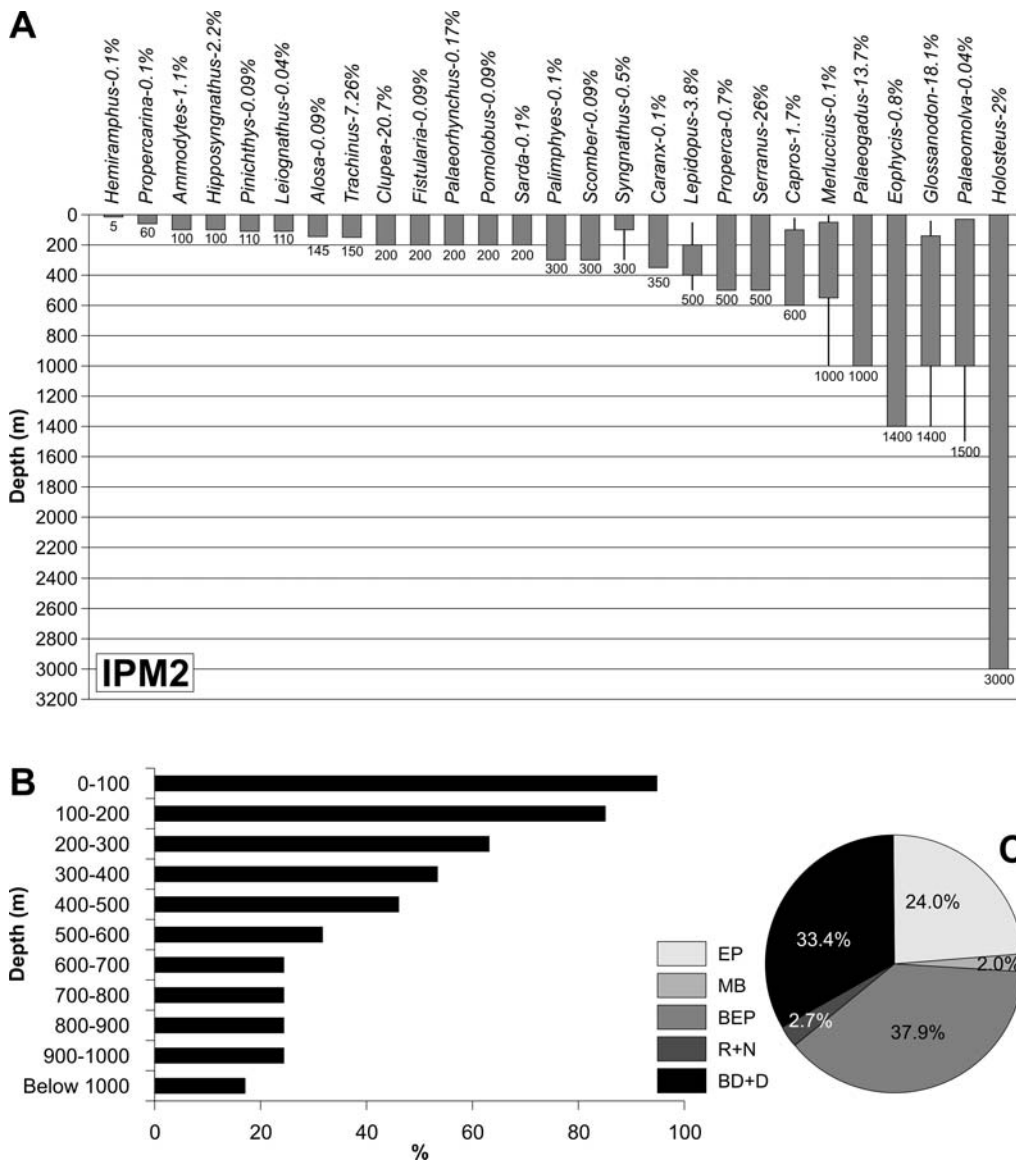


Fig. 22. Palaeobathymetry and palaeoecology of the IPM2 Zone fish assemblage. For explanations – see Fig. 21

only. In this zone, the presence of *Palaeomolva monstrata*, a species dwelling close to the bottom, was noted for the first time. The climate was similar to that of Zone IPM 4A, i.e. subtropical and tropical one, although characterised by constant presence of both eurytopic taxa, and those capable of surviving in a colder temperate climate (*Cetorhinus*, *Merluccius*, *Palaeogadus*, *Zeus*). The marine basin was an open one, and of depth comparable to that of Zone IPM 3.

Zone IPM 5

This zone (Fig. 26) is characterised by predominance of epipelagic forms (35.7%), including genera of *Sphyraena* and *Acanthocybium* which occur for the first time. Deep-water taxa, including new genera of *Nessorhamphus* and *Argyropelecus*, are not frequent (7.7%), similarly as those of fishes living close to the bottom (5.1%). Benthopelagic taxa (24.1%) comprise a new genus *Carpathichthys*, including index species *Carpathichthys polonicus*. Reef and neritic forms are represented by 27.4% of specimens. Domi-

nance of taxa preferring tropical and subtropical climate (e.g. *Holocentroides*, *Africentrum*, *Apostasis*, *Psenicubi-ceps*, *Pinichthys*) suggests climatic conditions comparable to those of zones IPM 4A and IPM 4. The above-mentioned insignificant proportion of deep-water forms is surprising and requires detailed interpretation which will be presented in the next chapter.

Zone IPM 6

The share of epipelagic fish in Zone IPM 6 (Fig. 27) is comparable to that in Zone IPM 5. Genus *Archaeus* appears for the first time among numerous taxa which include an index species *Syngnathus incompletes*. Deep-water forms compose the dominant group (45.1%). Most of them bear photophores and are capable of vertical migrations. There appear for the first time such genera, as: *Protomyctophum* and *Prohollandia*, and *Argyropelecus cosmovicii*, an index species of this group. The benthopelagic fish assemblage (15.8%) is taxonomically diversified. Forms associated with

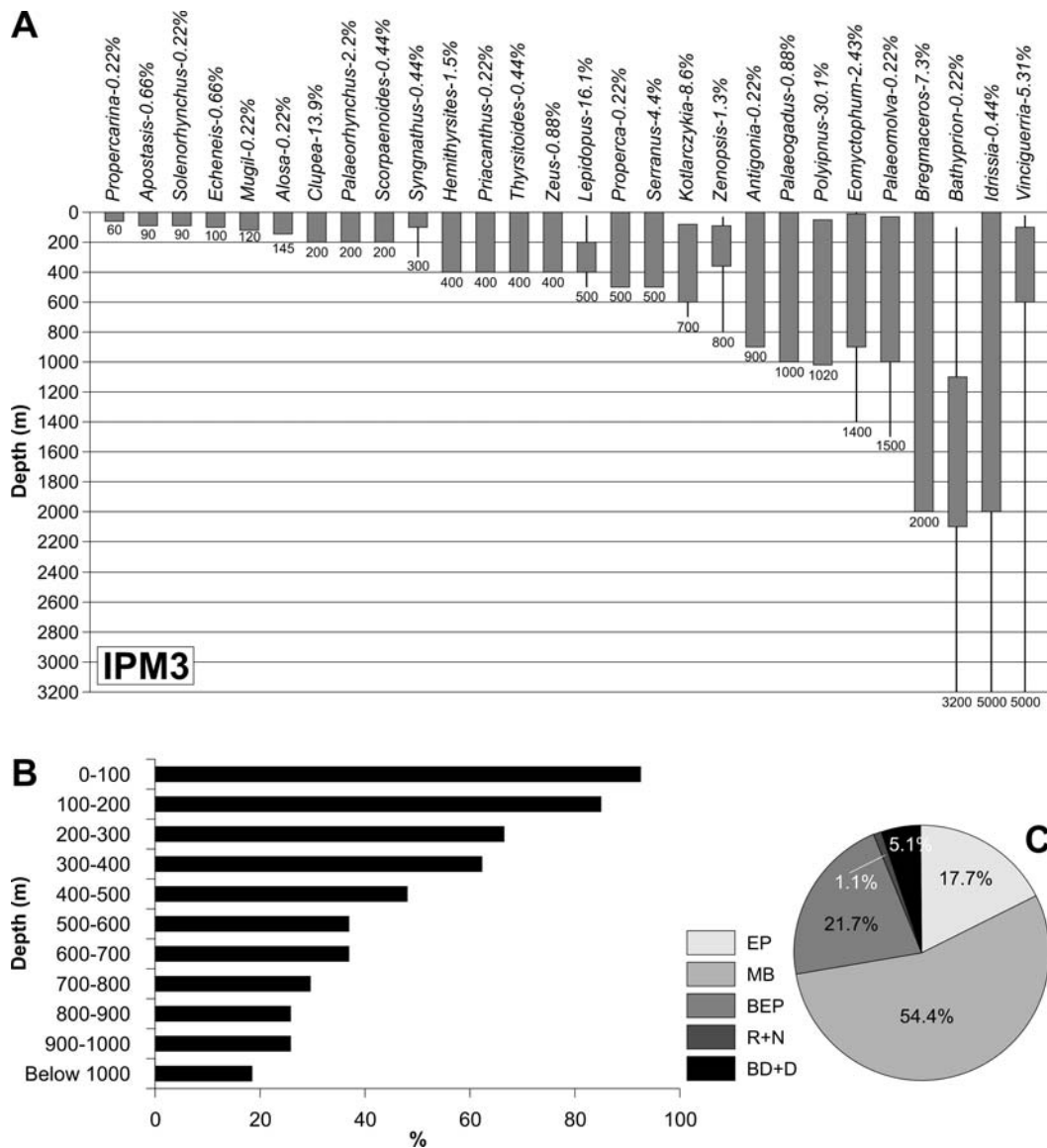


Fig. 23. Palaeobathymetry and palaeoecology of the IPM3 Zone fish assemblage. For explanations – see Fig. 21

reefs and littoral environment are infrequent (1.2%), although differentiated, similarly as the taxa associated with the sea bottom (2.4%), including genus *Paraberyx*. Basing on bathymetric preferences of the existing fishes, one can reconstruct a relatively deep, vast basin. The presence of numerous floating algal thalli and taxa belonging to families Syngnathidae and Antennaridae, as well as a representative of genus *Ammodytes*, occurring in this zone and presently observed in the Sargasso Sea, enables one to distinguish a new quasi-sargassum assemblage. Likewise in the previous zones, the most numerous are taxa associated with a warm, tropical and subtropical climate (e.g. *Acanthocybium*, *Apostasis*, *Echeneis*, *Psenicubiceps*, *Pinichnthus*, *Holocentroides*, *Africentrum*, *Serranus*, *Capros*, and others). There also occur common eurytopic forms (representatives of families Clupeidae and Scombridae), alongside with taxa capable of surviving in a colder, temperate climate (*Ammodytes*, *Palaeorhynchus*, *Zeus*, *Palaeogadus*, *Merluccius*). This may point to a persisting warm climate, in which forms tolerant to climatic oscillations could survive.

Zone IPM 7

Epipelagic fishes constitute nearly 50% of the assemblages of Zone IPM 7 (Fig. 28), being dominated by genera *Clupea* and *Syngnathus*. Deep-water fish comprise 36.1%, and benthopelagic ones include 11.3% of the entire set. Reef and neritic forms are infrequent (2.2%), similarly as those dwelling near the bottom (1.3%), including a new genus *Notidanus*. Basing on climatic preferences of the present-day taxa, related to the fossil ones, one can infer that compared to Zone IPM 6 the climate did not change, being still warm (subtropical and tropical) and bearing fishes of wide ecological tolerance.

Zone INM 1

The onset of the Miocene is represented by ichthyofaunal zone INM 1 (Fig. 29), whose deposits bearing a poor fish assemblage have been identified at two localities. The epipelagic forms are most common (68.9%), with dominant taxa of the family Clupeidae. The deep-water forms are absent. The remaining ecological groups are represented by:

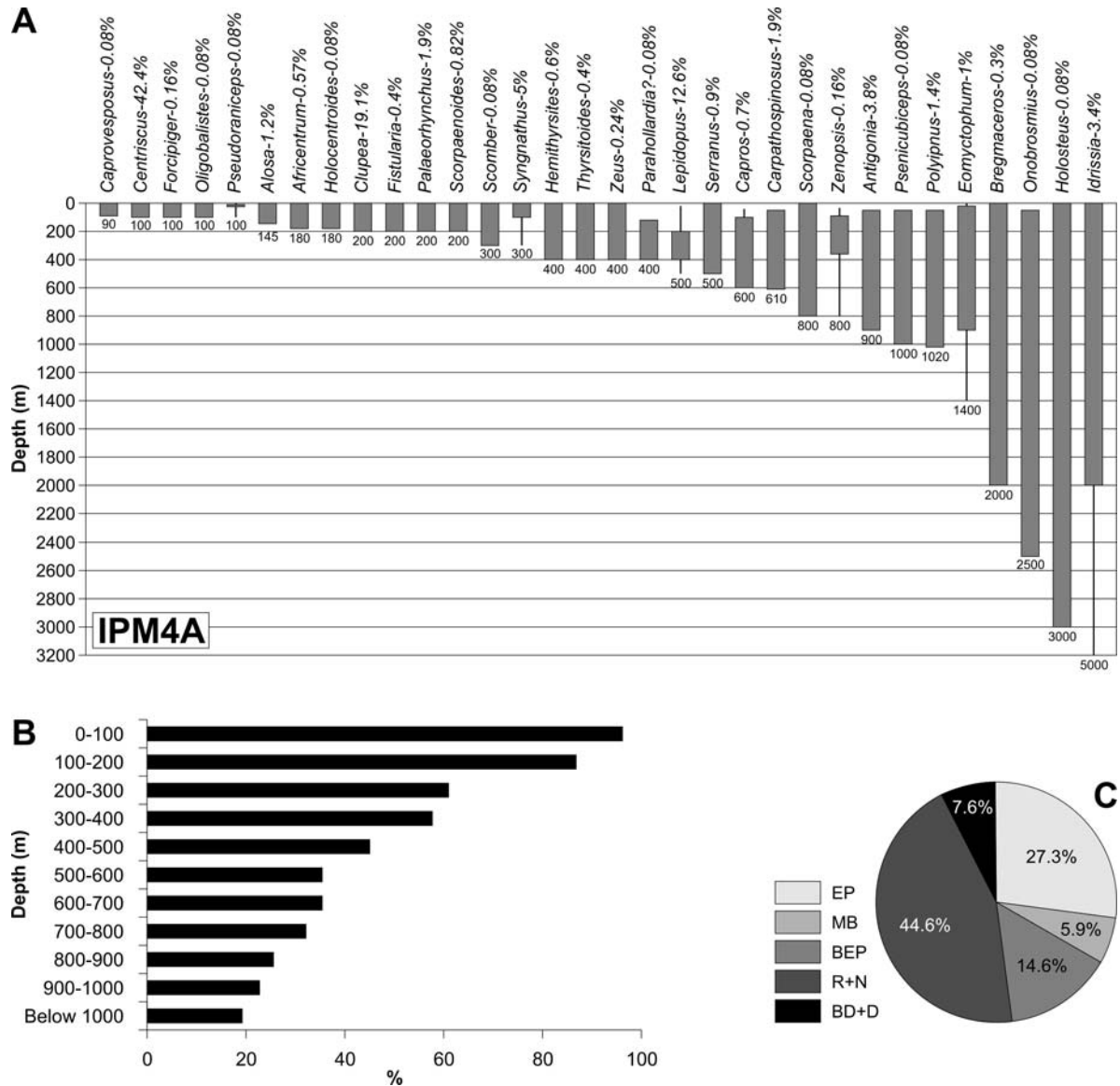


Fig. 24. Palaeobathymetry and palaeoecology of the IPM4A Zone fish assemblage. For explanations – see Fig. 21

bathy-demersal and demersal forms (0.7%), including genus *Gobius*, appearing for the first time, benthopelagic forms (28.4%; *Leiognathus*, *Lepidopus*, *Merluccius*), and those of reef and neritic environments, including an index species *Caranx gracilis* (2%). This may point to a considerable shallowing of the basin, similarly as the presence of such genera, as: *Caranx*, *Gobius*, and *Leiognathus*, which constitute more than 18% of the entire assemblage. The climate was still subtropical or tropical.

General characteristic of the studied fish assemblage

The Carpathian basin of the Tethys includes more than 130 fish taxa, represented by both extinct and present-day forms that belong to different ecological groups, associated with the changes in basin bathymetry and surface water temperature.

There occur epipelagic species, from which Clupeidae: *Clupea* and *Alosa* have been noted in all ichthyofaunal

zones. In the majority of these zones, *Syngnathus* and *Palaeorhynchus* are common genera. Deep-water species include, among others, photophores-bearing fishes (Gonostomatidae, Myctophidae) which are represented by genera occurring in most zones: *Polyipnus*, *Eomyctophum*, and *Vinciguerra*.

Benthopelagic fish occur throughout the section. Each zone includes the representatives of genus *Lepidopus*, while those of *Merluccius*, *Hemithyrsites*, *Thyrstitoides*, or *Palaeogadus* are less common.

Fishes closely associated with the sea bottom occur as solitary taxa in all the zones, the common genera being *Serranus* and *Scorpaenoides*.

All the zones include those fish which dwell reef environments, including frequently occurring genera, like: *Africentrum*, *Holocentroides*, and *Caranx*.

Special attention should be given to a shallow-water fish assemblage of the IPM 6 Zone, bearing the family Syngnathidae, Antennariidae, a representative of the genus

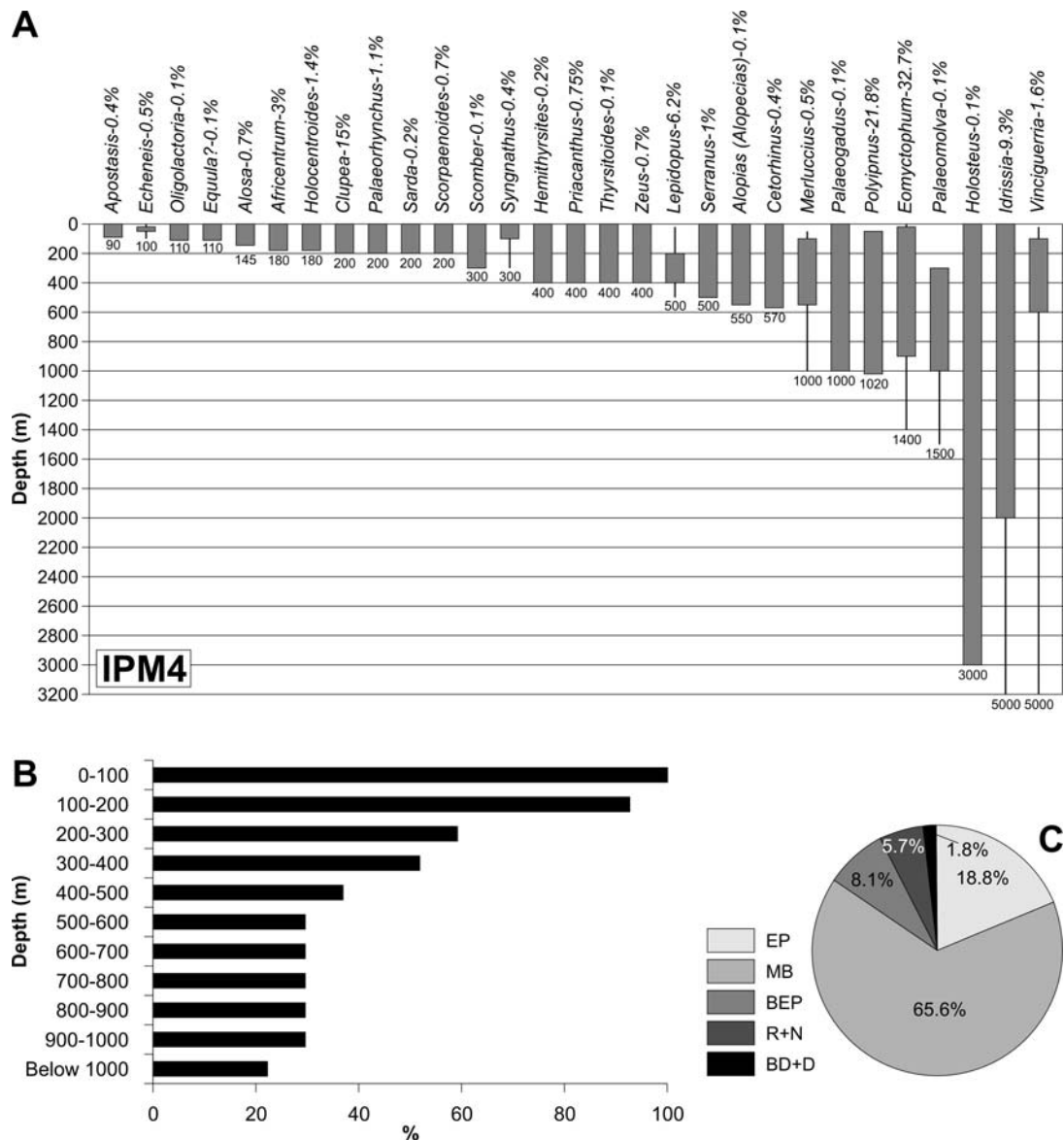


Fig. 25. Palaeobathymetry and palaeoecology of the IPM4 Zone fish assemblage. For explanations – see Fig. 21

Ammodytes, and deep-water taxa of families: Gonostomidae, Myctophidae, Sternoptychidae, together with abundant algal thalli, similar to those which occur in the Sargasso Sea. This assemblage has been identified as a quasi-sargassum one. According to Jerzmańska and Kotlarczyk (1975, 1976), the Tethys basin was the original place wherefrom this association had migrated into the Atlantic before the end of the Miocene.

The genera: *Centriscus*, *Caranx*, *Serranus*, *Capros*, *Acanthocybium*, *Apostasis*, *Echeneis*, *Psenicubiceps*, *Piniichthys*, *Holocentroides*, and *Africentrum* are important indicators of tropical and subtropical climate, while *Ammodytes*, *Palaeogadus*, *Cetorhinus*, and *Propercarina* belong to cold climate indicators.

Differences in species composition of the same genera within individual zones have also been observed. The extinct species are replaced by new ones, including index species which determine the extent of ichthyofaunal zones.

The ichthyofaunal assemblages of individual zones re-

flect environmental changes that proceeded in the Tethys marine basin of the Polish Carpathians since the latest Eocene to the beginning of Miocene times. These changes included those in climate, bathymetric and thermal properties of the basin, as well as migration and succession of ichthyofauna.

CHANGES OF ECOLOGICAL ASSEMBLAGES OF ICHTHYOFAUNA IN THE MENILITE-KROSNO SERIES BASIN: A MODEL

Detailed palaeoecological analysis of species, genera, and families of fish housed in the Carpathian collection, presented in the previous chapter, allows for ecological characteristics of fish assemblages occurring in the distinguished zones. Careful scrutiny of the entire collection con-

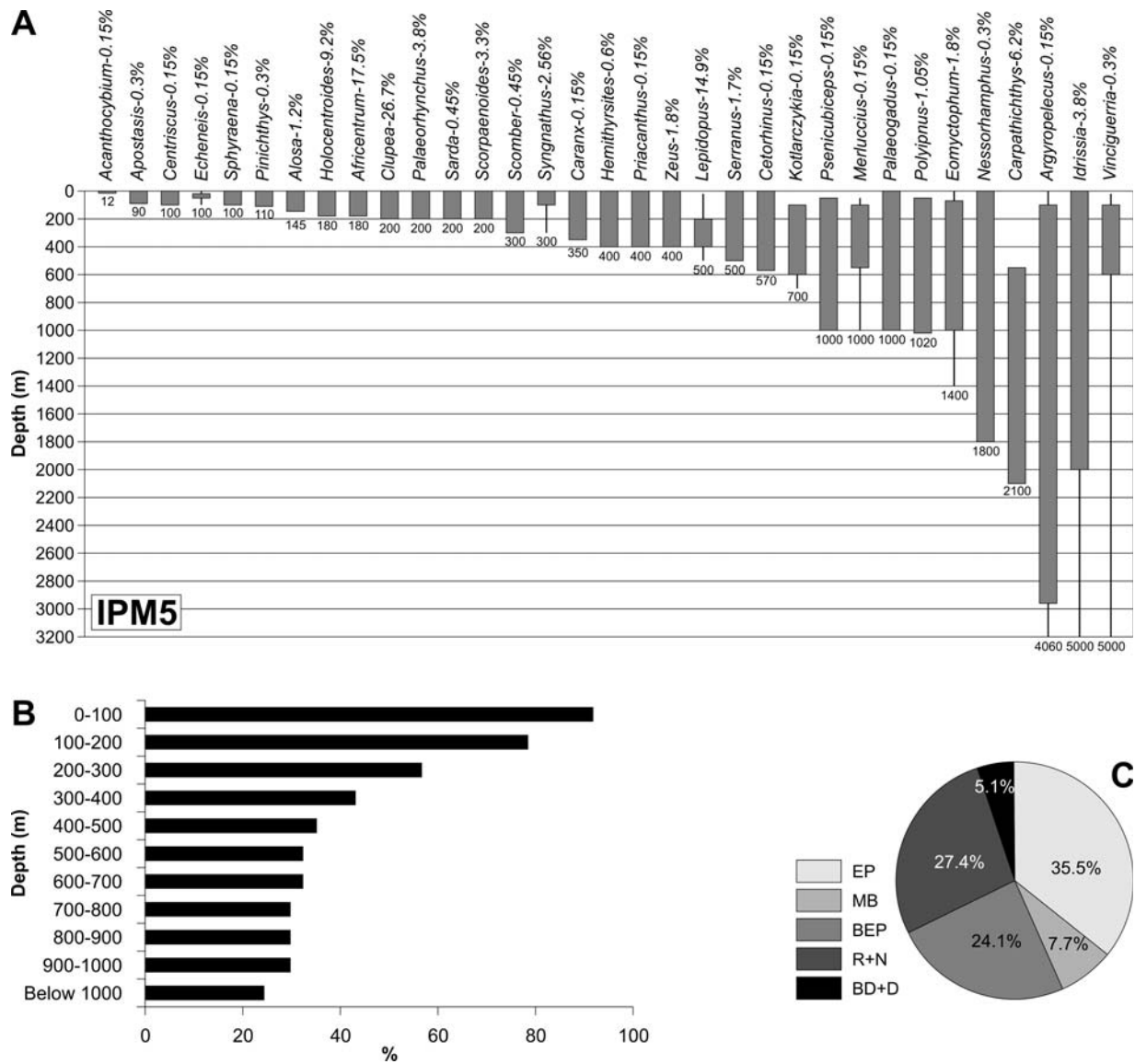


Fig. 26. Palaeobathymetry and palaeoecology of the IPM5 Zone fish assemblage. For explanations – see Fig. 21

firmed the sequence of assemblages: LBA, NSA and UBA, already observed in the late 1960s, and helped to identify strong differentiation within UBA, as well as to distinguish another, i.e. the youngest one, neritic-sublittoral fish assemblage (UNSA). The enclosed diagrams (Figs 21–29), illustrating the ecology of every zone, are biased by a certain portion of theoretical considerations.

Diagrams of group A portray, following published sources, standard depth intervals within which contemporary fish genera are being caught, as well as the alleged extents of fossil counterparts of the latter. Thin lines mark the extents either inferred from solitary fishing campaigns, or suggested by single authors. These depth intervals can indicate, although without absolute certainty, the extent of Oligocene taxa and indirectly point to basin palaeobathymetry.

Diagrams of group B, illustrating in detail the epimesopelagial zone only, provide information about the percentage of taxa within individual 100-m-long depth inter-

vals, although following the extents marked in diagrams A. If these extents were in fact shorter than those marked in diagrams A, then percentages of the lower-situated intervals should also be smaller.

Diagrams of group C show proportions of the distinguished ecological groups within assemblages of the respective zones. However, one has to take into account arbitrary way of classifying a taxon to a group in case of genera occupying different environments. The following criteria were used: taxa occurring both in the EP and MB zones were included into group MB, taxa living in the MB and BEP zones were assigned to group BEP, taxa occurring in the BEP and BD+D zones were included in group BEP, whereas those inhabiting the BD + D and R + N zones were included into group BD + D. Moreover, diagrams constructed for zones IPM2 and IPM4A include also fishes exploited from individual layers: JE-1 and PS5-42, respectively, representing exceptional events.

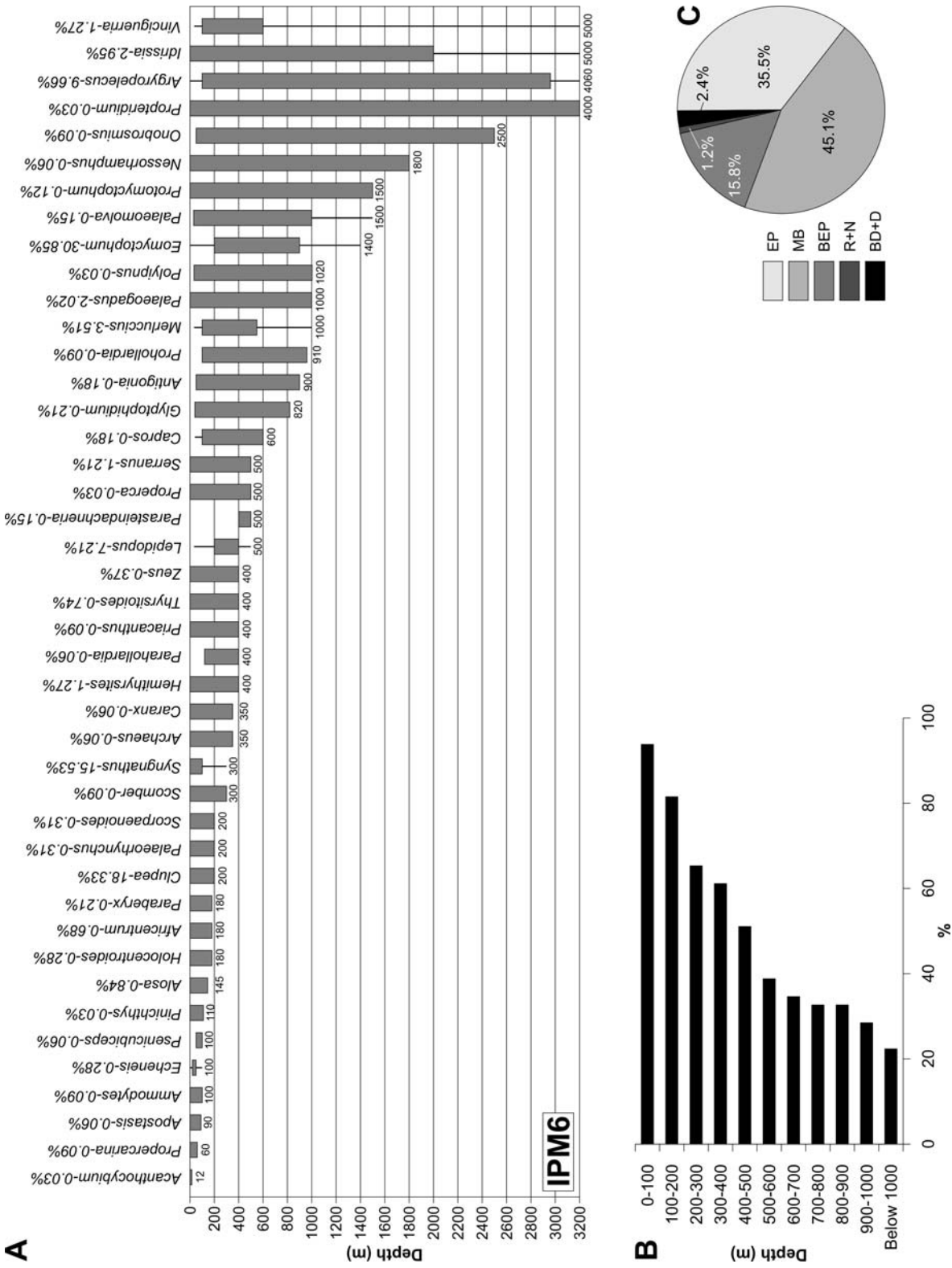


Fig. 27. Palaeobathymetry and palaeoecology of the IPM6 Zone fish assemblage. For explanations – see Fig. 21

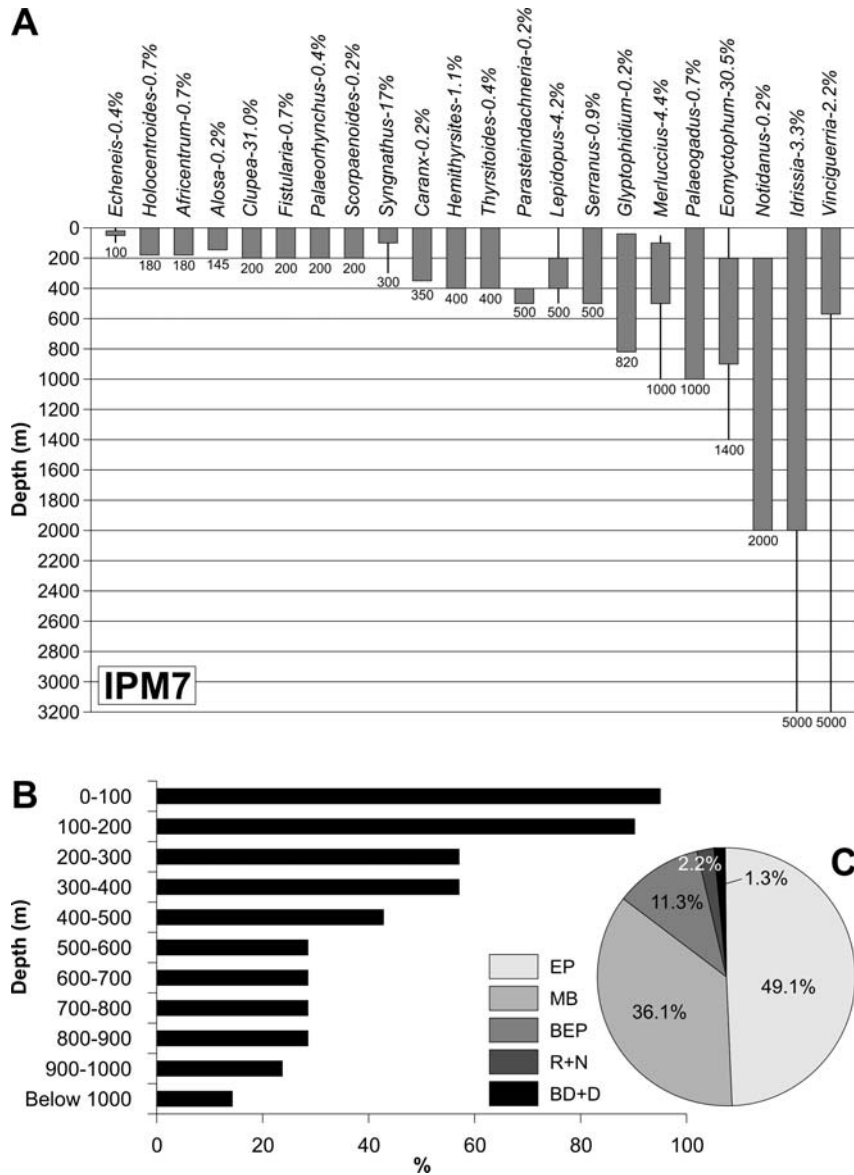


Fig. 28. Palaeobathymetry and palaeoecology of the IPM7 Zone fish assemblage. For explanations – see Fig. 21

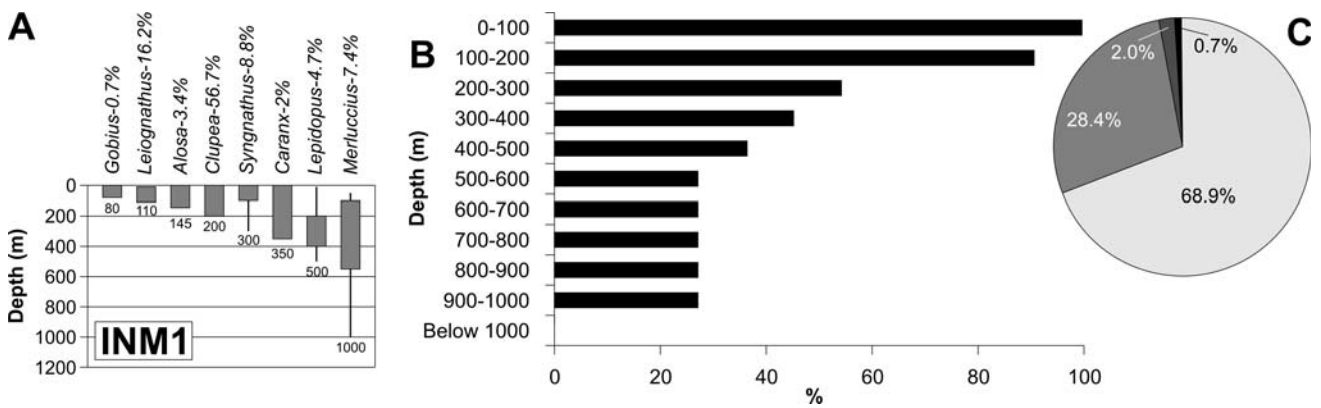


Fig. 29. Palaeobathymetry and palaeoecology of the INM1 Zone fish assemblage. For explanations – see Fig. 21

The abundant material presented on Figures 21–29 cannot be easily interpreted. To clarify the picture of assemblage changes with time, a simplified diagram (Fig. 30) was constructed showing those taxa whose percentage was at least 1% in a given zone. Each taxon is marked by a different colour: shades of blue denote epipelagic fishes (EP), green – meso- and bathypelagic fishes (MB), purple – benthopelagic fishes (BEP), brown – bathy-demersal and demersal fishes, and yellow – reef and neritic fishes. All less frequent taxa were shown in white. The latter represented different ecological environments, but their omission did not seriously affect the presented ecological spectrum of a zone.

Vertical hatchure marks the share of index taxa within the distinguished genera. The diagram shows the composition of zones IPM2 and IPM4A twice, both including and excluding fishes associated with the *Trachinus* and the second *Centriscus* events. In both cases it becomes evident how taking into account single, mass occurrences of fish belonging to one genus distorts ecological picture of the entire zone. When applying the above-mentioned criterion of showing more numerous (>1%) taxa only, less frequent taxa, like: *Eophycis* in zone IPM2, or *Africentrum*, *Capros* and *Scorpaenoides* in zone IPM4A, disappear from columns portraying a given event.

The diagram also shows that all the zones bear a large proportion of representatives of epipelagic (EP) and benthopelagic (BEP) fishes only. Meso- and bathypelagic (MB) fishes are frequent in zones IPM1, IPM3, IPM4, IPM6 and IPM7; infrequent in zone IPM4A; sporadic in zone IPM2; and absent from zone INM1. Bathy-demersal (BD) and demersal (D) forms make up a large proportion in zones IPM2 and IPM4A; small proportion in zones IPM3 and IPM5; and minor proportion in zones IPM4, IPM6 and IPM7 (not exceeding 1% in zones IPM1 and INM1). Reef and neritic fishes constitute an important share (27.4%) in zone IPM5 only, whereas in zones IPM1, IPM4A (without specimens associated with the 2nd *Centriscus* event), and IPM4 their proportion is ca. 6%; and in zone INM1 does not exceed 2%.

A synoptic overview of ecological content of zonal assemblages allows one to distinguish three different compositional patterns. The zones of comparable ecological pattern were grouped together (Fig. 31) to visualize the existing contrasts.

The first pattern is represented by zones IPM1, IPM3, IPM4, IPM6, and IPM7, i.e. those which belong to both bathypelagic assemblages. Clearly dominant within these assemblages are fishes of open-ocean zones, including mostly meso-bathypelagic ones, whereas a large amount (8.1–16.6%) is attained by benthopelagic fishes.

The second, a little more differentiated, pattern occurs in zones IPM2, IPM4A, and IPM5, i.e. in the neritic-sublittoral one and the two UBA zones. Of particular importance is the dominance of benthopelagic, demersal, bathy-demersal, reef, and neritic fishes (attaining nearly equal proportions in zone IPM4A) compared to meso-bathypelagic fishes. The latter compose 2 to 9.5% of the total.

The third pattern appeared in the youngest, INM1 zone only. Epipelagic fish comprise here nearly 70%, and ben-

thopelagic ones attain ca. 30% of the total. This zone is completely devoid of meso-bathypelagic fish; therefore, the assemblage deserves to be distinguished as the upper neritic-sublittoral one (UNSA).

Zonal assemblages of the first pattern

Both diagrams illustrate well an hypothesis that the basin filled with those Menilite Fm. deposits which bear assemblages of the first pattern was a deep-water basin, with well-developed and rich meso-bathypelagic ichthyofauna. A permanent component of the generic composition were *Eomyctophum* and *Vinciguerria*, and in UBA also *Idrissia* and *Polyipnus* (below IPM6 Zone). The remaining genera of this ecological group occurred sporadically in individual zones, providing suitable material for ecostratigraphy.

Depth intervals dwelled by such genera, as: *Vinciguerria*, *Idrissia*, *Argyropelecus*, and *Scopeloides*, exceeding the lower limit of the meso-bathypelagic zone (estimated by different authors at either 1,100 m, 1,500 m or 2,000 m), enable one to suppose that the Menilite basin was deeper than 2,000 m. This conjecture is also supported by figures related to the lower depth intervals dwelled by some benthopelagic taxa.

Another permanent and important component of the discussed zonal assemblages were: a benthopelagic *Lepidopus*, usually dwelling above the slope and below the shelf break to a depth of 400–500 m; and in UBA: infrequent *Hemithyrssites*, preferring similar conditions, *Merluccius*, whose importance increased in the sixth and seventh zones, as well as *Palaeogadus*. The last two genera occurred to a depth of 1,000 m. These benthopelagic fishes are to be found all over the study area, implying that they must have been transported upon the lower part of the continental rise and bottoms of the SKU or SU trenches by currents flowing from higher-situated biotopes.

In a similar way, one can explain why on a vast basin bottom there occur demersal and bathy-demersal fishes which dwell waters of the sublittoral zone and those of higher parts of the slope to a depth of 500 m; as well as fishes of the neritic zone, together with the reefal ones. These represent a minor component (1 to 6%) of deep-water tanathocoenoses. The pelagic Jasło Limestones exposed at sites located in the middle of SU (Sobniów – SO) and SKU (Łubno-Łazek – ŁŁ) trench bottoms include adult representatives of reefal environments, like, for instance, *Holocentroides* and *Africentrum*, the occurrence of which can be explained by the activity of marine currents of different types (like presence of a frog skeleton in the Jasło Limestone at Sobniów; A. Jamróz coll.; M. Bieńkowska, *pers. comm.*).

The above presented formation of ichthyofaunal tanathocoenoses of the Menilite Fm. is complicated by the appearance of assemblages of the second type. This process requires a more thorough explanation. On the other hand, appearance of the **third pattern** (UNSA) is understandable in the light of infilling of the SKU trench by deposits of the Krosno Fm. This deposition could lead, at the final stages of submarine fan development, to basin shallowing and elimination of deep-water fishes. A marked share of taxa tolerating brackish conditions (*Gobius*, *Leiognathus*, *Caranx*)

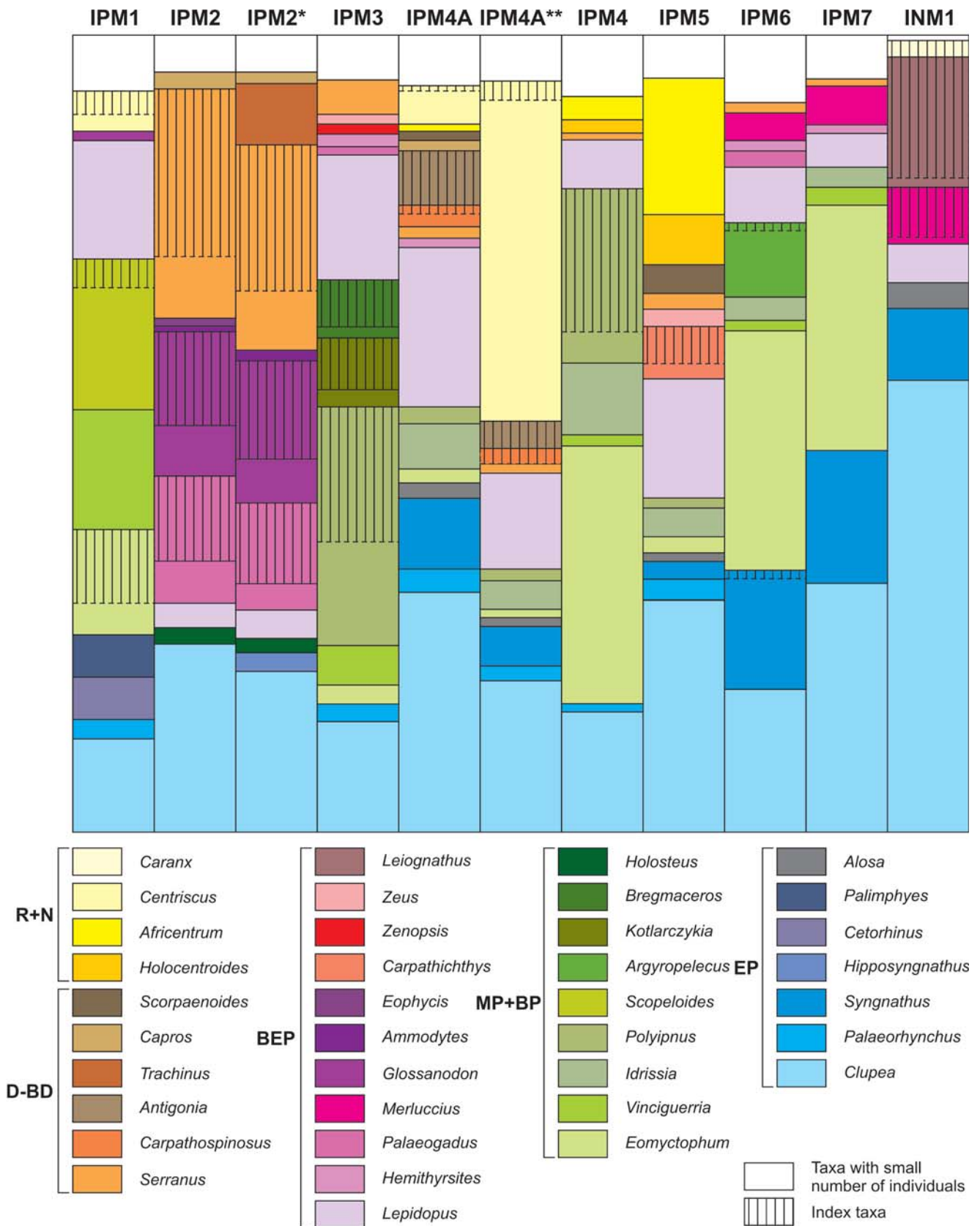


Fig. 30. Percentage of fish genera of different ecological groups occurring most frequently within the zones (only genera exceeding 1% are taken into account); height of zonal column denotes 100%. Symbols of ecological groups as on Fig. 21. Zonal symbols marked by asterisks indicate those generic spectra which include fishes derived from layers representing mass fish mortality. Vertical hatchure marks the share of index taxa within each genus

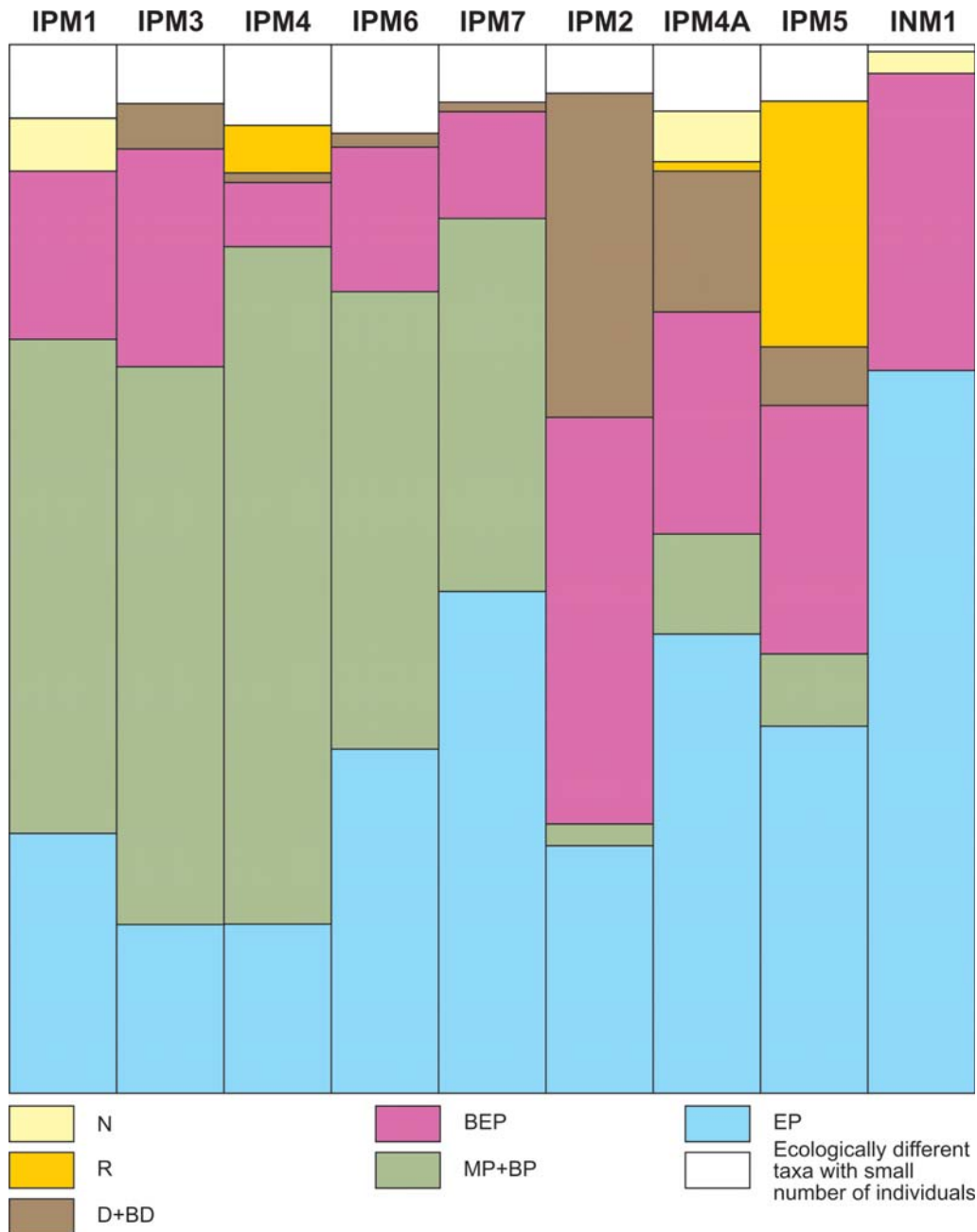


Fig. 31. Three patterns of ecological composition of ichthyofaunal zones in the Polish Carpathians: 1 – IPM1 – IPM7: zones dominated by epipelagic and meso-bathypelagic fishes, 2 – IPM2 – IPM5: zones dominated by bottom, near-bottom, and neritic fishes, 3 – INM1: zone bearing exclusively shallow-water fishes; MP – mesopelagic fishes; BP – bathypelagic fishes. Other explanations – see Fig. 30

within the third pattern assemblage is compatible with the presence of fresh-water diatoms in the Leszczawka Mbr (Kotlarczyk, 1982).

Zonal assemblages of the second pattern

Zone IPM2

Regarding fish assemblages of the second pattern, interpretation of the IPM2 Zone assemblage raises the greatest difficulty.

At the end of the 1960s, successive occurrence of sepa-

rate ecological assemblages composed of either shallow- or deep-water taxa was recognised, and different possible causes of their origin were discussed (Jerzmańska & Kotlarczyk, 1968). Finally, the appearance of a shallow-water assemblage between deep-water ones was interpreted as a result of a shallowing of the Carpathian basin, the depth of which was estimated at ca. 1,000 m. The inferred shallowing by 200–300 m was considered responsible for the elimination of bathypelagic taxa from the basin.

It has to be remembered that at that time the presence of deep-water fishes in the IPM2 Zone assemblage IPM2 (*Holosteus*) was not recognised, and the benthopelagic

Glossanodon was considered by Cohen (1958) as recently dwelling in the near-shore zone (90–200 m) and migrating into the mesopelagic zone in spawning season only.

The origin of this zonal assemblage has been dealt with several times (Kotlarczyk, 1975; Jerzmańska & Kotlarczyk, 1979, 1991; Kotlarczyk & Jerzmańska, 1988a). Since 1968, S. Dżułyński has been proposing a concept of elimination of deep-water fish from the basin due to anoxic conditions prevailing in deeper parts of the water column. This hypothesis has been accepted since the 1920s to explain the origin of similar fish assemblages in the Caucasian basin (see, for instance, Daniltshenko, 1960). The presented arguments, however, did not lead authors to change their views, and a concept of basin shallowing appeared to have been supported by a global sea level fall in the Early Oligocene (Kotlarczyk & Jerzmańska, 1988a). This fall was in fact documented for the boundary between the Early and Late Oligocene (Vail *et al.*, 1977), but the quoted authors (Kotlarczyk & Jerzmańska, 1988a) inferred that it could have started earlier in the studied basin, like in some other parts of the world.

Nevertheless, important augmentation of the ichthyological material derived from all exposures of the IPM2 Zone (2,583 specimens, including 2,356 determined to the level of either species or genus) necessitates re-evaluation of previously suggested bathymetric intervals of this assemblage in the studied basin, and re-consideration of its origin. A superficial comparison of diagrams showing depth intervals dwelled by fishes comprised in the IPM1 (Fig. 21A) and IPM2 (Fig. 22A) zonal assemblages may lead to a conclusion that the latter are similar and that there is no need to distinguish a neritic-sublittoral assemblage.

It is important to note, however, that during this zone only pelagic deep-sea fish genera *Eomyctophum* and *Vinciguerria* disappeared. These genera, as marked on the diagram (Fig. 21A), can also dwell shallow waters. Representatives of the two families, to which the above genera belong, namely: Myctophidae and Photichthyidae, require a possibility of easy migration into lower parts of the mesopelagial, and when this migration is not possible, they disappear from the water column.

Another question is the presence of a benthopelagic genus *Glossanodon* which prefers nearly identical depth intervals as *Eomyctophum*. At present, family Argentynidae, to which this genus belongs, is assigned to deep-sea fishes. However, extremely important are comments by Weitzman (1997; p. 57) regarding this family and genus: "*Argentines. These fishes have eggs and larvae that are pelagic. The adults are commonly taken at the margins of the continental shelves. There are two genera, Argentina and Glossanodon, with a total of about 19 species. Some species of these large-eyed fishes apparently reach depths of nearly 1000 m but most usually occur at shallower depths*" (all underlines by J. K.). The comment implies that these fishes require the first few hundreds of metres of water only.

The same applies to a few other representatives of benthopelagic fishes. Nearly equally numerous is *Palaogadus*, a representative of the family described by Weitzman (*op. cit.*; p. 64) as: "*The Merluccidae, or hakes, are mostly shallow to deep-water continental shelf and slope fishes, but a*

few reach depths 1000 m." This author similarly describes the biotope of a recent representative of family Phycidae, which in our fossil material is represented by *Eophycis*, and at present includes 27 species, from which only three penetrate greater depths: "... *Urophycis tenuis* is known from 980 m, *although it is usually found around 180 m*" (Weitzman, *op. cit.*; p. 65).

A benthopelagic *Lepidopus* of Trichiuridae family, fairly numerous in the IPM2 Zone, is most frequently found close to the shelf break and upon upper slope, although may occur in the epipelagial as well. Another genus of this group, *Ammodytes*, does not exceed a depth of 100 m.

Another important component of the discussed zone, i.e. demersal fishes, is represented first of all by genus *Serranus* and, to a lesser degree, by related to it extinct genus *Properca*. The Serranidae family dwells mostly shelf and the upper part of slope, like Caproidae family which is represented by fairly numerous *Capros*. These shelf and upper slope genera are accompanied by Piscivores – *Caranx*, dwelling waters to a depth of 350 m, and *Holosteus* which can be found to a depth of 3,000 m. Given the lack of mesobathypelagic fish, this piscivorous predator must have occurred together with the above-mentioned fishes of the upper part of the slope. It is not by accident that abdominal cavities of two specimens of *Holosteus* contained swallowed fishes, one belonging to Serranidae and the other one to Argentynidae (Bieńkowska, 2004; p. 188, fig. 20).

Undoubtedly, the IPM2 Zone assemblage should be considered a shallow-water one, and the lower boundary of its occurrence should be placed at a depth of ca. 500 m. It is worth to note that recent ichthyologists include to deep-sea fish taxa those dwelling below 500–600 m depths, or only those which penetrate waters below this boundary (see, for instance, Weitzman, 1997; p. 43).

A question remains how this ecological assemblage was formed. Two possibilities can be considered: 1. due to basin shallowing, or 2. due to elimination of deep-water fish as a result of periodical formation of anaerobic conditions at depth.

Theoretically, the first option could have occurred owing to different factors: (1) tectonic movements uplifting basin bottom, (2) filling the basin by sediments, (3) eustatic movements, and (4) basin dessication; while the second option may have resulted from short-term isolation of the basin.

According to A. Jerzmańska, the basic difficulty in accepting the second possibility consisted in a vast spread of the tanathocoenosis of the IPM2 assemblage throughout the bottom of the Menilite basin, i.e. at a distance of a few hundred kilometres, necessitating a long-distance and, hence, long-term transport of dead fish from the shelf break to the deepest parts of the basin. Long-distance transport should have led to dismembering (e.g. by boulders) and decomposition of fish bodies, while a great deal of undestroyed (more than 25%) skeletons in the collection appears to indicate an autochthonous character of the assemblage (Jerzmańska & Kotlarczyk, 1973). Unfortunately, the content of layer E₁ at Jamna Dolna was not interpreted correctly. This layer, only 1 cm thick, contains i.a. very numerous two shallow-water taxa: the extinct *Hipposyngnathus*, associ-

ated with near-shore waters like seahorses of the same family Syngnathidae, and a demersal, sublittoral *Trachinus*, frequently represented by young specimens. Such a composition calls for a comparison of layer E₁ to the assemblages described by Lo Bianco (1909) as “fragaglia” from the Bay of Naples, and for using this similarity as another indicator of basin shallowing. However, it has not been recognised that solitary occurrence of this assemblage, presently interpreted as the *Trachinus* event, does not testify to extreme basin shallowing, but rather to a possibility of long-distance fish transport: from near-shore embayments at a distance of at least 30 km towards open sea.

New facts and interpretations force us to re-discuss the origin of the IPM2 Zone assemblage. Let us begin with a review of the above-mentioned causes of the alleged basin shallowing.

(1) Assigning formation of NSLA to the lower part of biozone [NP23] at ca. 30–31 Ma enables one to conclude that no important folding close to the study area took place at that time.

(2) Detailed sedimentological observations point to stable, although not intensive development of deep-sea fans; except for small-scale deposition of the Huwniki Sandstone. This deposition could not lead to basin shallowing; and the deposits bear no traces of structures typical of shallow basins (up to 100 m deep). Ubiquitous occurrence of ripple cross-laminated sandstones bearing laminae composed of heavy minerals (tractionites; *sensu* Unrug, 1980), indicating palaeotransport direction parallel to inclination of the slope and continental rise, points to the presence of a deep sea and stable flow of heavy waters down the slope. Within DU and, in part, SU intensive deposition of flysch sediments of the Cergowa Mbr and Krosno Fm. took place at that time, although not causing basin shallowing all over the area.

(3) A minor global sea level fall took place in the discussed interval, between cycles T_{4.4} and T_{4.5}. The eustatic curve of Haq *et al.* (1988) (cf. Fig. 33), combined with a time-scale by Berggren *et al.* (1995) showing the ages of boundaries between biozones and stages, places this sea level fall at ca. 31 Ma and estimates its amplitude at 25–30 m only. This figure could not, of course, lead to the alleged basin shallowing that would have replaced the deep-water assemblage by a shallow-water one. However, the resulting shelf narrowing could have affected a shift of near-shore fish biocoenosis towards shelf break, wherefrom large quantities of fishes could have been easily transported *post mortem* into the basin.

(4) Separation of the Menilite basin from the remaining Tethys in subtropical climate at that time should have resulted in quicker evaporation, leading to basin shallowing. This problem was already raised during a discussion on the origin of the NSLA assemblage (Kotlarczyk, 1975).

Another likely scenario of formation of the NSLA assemblage should take into account a sequence of several factors which will be presented below.

(1) Tectonic development of the Western Tethys during the [NP23] biozone led to separation of a nearly isolated northern basin, which extended from the Alps through the Carpathians, Black Sea, Caucasus, up to the Aral Sea. A likely palaeogeography of this area was presented by Rögl

(1999, fig. 3). The northern basin was most probably linked with the principal, southern basin of the Western Tethys via the Slovenian corridor (Sc) only, whereas a connection with the North Sea was probably situated along the Rhine Graben. (2) The above mentioned sea level fall, although insignificant, could have led, given shallow Sc bottom, to a restriction in water influx from the southern to the northern Western Tethyan basins, and (3) accelerate dessication processes in the northern basin. (4) Re-opening of the connection restored the deep-water character of the Menilite basin and led to formation of the UBA.

An alternative scenario includes after event (1) formation of anaerobic conditions within the Menilite basin and favours the second option.

One should bear in mind that the formation of black sediments of the Menilite Fm. cannot be explained by permanent stagnation of basin waters, because the same black shales comprise deep-water fish assemblages, including the near-bottom ones. On the other hand, the basin was characterized by deep-water circulation (tractionites, turbidity currents) and, probably, also upwelling (Jerzmańska & Kotlarczyk, 1973).

Formation of black shales should rather be explained by insufficient amount of oxygen in sea water, the oxygen being quickly used to oxidize large quantities of organic matter hosted in sediments. These processes led to preservation of anaerobic conditions both within the sediment and, periodically, also in the lower part of the water column. Partly isolation of the basin could have also caused a smaller influx of oxygenated ocean waters via Sc. Possible excess of evaporation over precipitation and reduced supply of oxygen transported to the bottom with the material feeding submarine fans could have extended the range of anaerobic zone high above the bottom, despite still active quasi-estuarine circulation in the basin. The shallow-water assemblage of IPM2 Zone bears exclusively marine fishes, indicating that estuarine circulation which would have led to water stagnation was not possible. It is worth to note that observations of nannoplankton assemblages suggest a decreased salinity of near-shore waters of the Menilite basin. These suggestions pertain to an episode of JLH formation during NP24 biozone (Bubik, 1992), and to the area of deposition of the coccolith Dynów Marls in the lower part of biozone NP23 (Krhovský, 1981, 1985; Stranik *et al.*, 1991), i.e. during the time of occurrence of deep-water fish.

This discussion implies that both scenarios of formation of the IPM2 assemblage are theoretically possible, although the second option appears to be a more plausible one.

Zone IPM4A

Regarding zonal assemblages of the second pattern, the easiest explainable is the origin of the generic-quantitative spectrum of Zone IPM4A. The assemblage of this zone, first described in this paper, was found exclusively in deposits of SSU. As was already mentioned, green-grey and brown-banded sediments of the Šitbořice Mbr were formed upon slopes of a submarine ridge. According to Parin's (1988) terminology, biotopes of ichthyofauna of these ridges bear names accompanied by a prefix “thalasso”. Hence, upon slopes we have: thalasso-mesobenthopelagial (TMB) and

thalasso-bathypelagic (TBB), whereas upon ridge shallows: thalasso-epipelagic (or pseudoneritic pelagic – PNP) and thalasso-epibenthic (TEB). Following configuration of the basin bottom, tanathocoenoses formed on the slope of the Subsilesian Ridge (accessible to observation now) could have included (and they did) fishes derived from different biotopes of different depth intervals upon the ridge: epipelagic EP (44%), PNP and reef environment (6%), MB (9.5%), TMB and TBB (21%), as well as TEB and bathy-demersal (13%) zones (Fig. 30).

A similar zonal assemblage should have occurred on the other subcontinental slope, the upper part of which was probably preserved in BPU. It is likely that a reflection of such basin bottom configuration are infrequent fishes of the reef-neritic and BEP zones, which were found in a section of the Menilite Fm. at Kniażyce (KN).

The above considerations lead to a conclusion that distinctness of the IPM4A zonal assemblage does not result from changeable environmental conditions throughout the Menilite basin, but from distinctness of conditions prevailing on the slope of a submarine high, compared to those upon the bottom and continental rise at the time of formation of zonal assemblages of the first pattern. Hence, one should not expect this assemblage to occur on the SKU trench bottom, although it cannot be excluded that specimens of some representatives of the Zone IPM4A assemblage, including index taxa (not found up to now), could have been transported there.

An exceptional event recorded in sediments of the IPM4A Zone is mass occurrence of fishes that belong to at least two species of *Centriscus* in layer 42 of exposure PS₅ at Przysietnica, and in one layer of exposure WZ₆ at Wujskie. This occurrence of *Centriscus*, as well as in five other layers above and below layer 42 at Przysietnica, is not related to nannoplankton bloom, since the Wujskie coccolith limestones occurring nearby do not contain these fishes.

The presence of fish population of Centriscidae family, frequently dwelling reef-neritic environments like, for instance, that surrounding the Seychelles, NE of Madagascar, can be explained very well by their burial place on the slope of the Sanok Cordillera submarine high; while exceptional abundance of fishes in layer 42 should be related to a mass mortality event.

Zone IPM5

The composition of the assemblage of the last, atypical IPM5 Zone of the second pattern is very interesting. This assemblage includes fishes collected mainly at exposures representing continental rise (Brzuska Syncline – KIII, HB₆, BR₁₁, BR₃₄, BH₃) and the central part of the SKU trench (Siemowica – SE I_{2,3}), being supplemented by a not numerous set of specimens from Przysietnica (PS₁) exposure, which represents the slope of a submarine high. This assemblage represents first of all a taphocoenosis formed at the bottom of a deep basin (Figs 26, 30, 31).

Compared to Zone IPM4A (excluding fishes derived from layer PS₅₋₄₂), meso-bathypelagic fish are here less frequent, whereas bathypelagic ones are somewhat more numerous. The share of demersal fish is reduced by a factor of three, while that of the neritic and reef fish is four times in-

creased. Particularly important is abundance of fishes derived from the last environment, not encountered in the assemblages of other zones, as well as a large proportion of representatives of a deep-water family Alepocephalidae among bathypelagic fish. It is worth to add that in a similar stratigraphic position (i.e., between the JLH and Lopyanka Mbr) in the Eastern Carpathians, in the Cieczwa (Tshetshwa) River section, a representative of another deep-water bathypelagic family – Macrouridae (Horbatsh, 1961) has been found.

Meso-bathypelagic fish, mostly: *Idrissia*, *Eomyctophum*, *Polyipnus*, and few other genera, which form a background of the zonal assemblage, undoubtedly point to a deep basin.

The assemblage of shallow-water fishes (near-shore, neritic-sublittoral, and reefal ones) is composed of *Holocentroides*, *Africentrum*, *Sarda*, *Apostasis*, and other genera (Fig. 26). A short comment seems necessary at this place. A. Jerzmańska in her last papers (Jerzmańska & Kotlarczyk, 1988; Kotlarczyk & Jerzmańska, 1988a; Jerzmańska, in: Kotlarczyk, 1991b) firmly maintained that forms determined by her as *Africentrum moldavicum* should be treated as *Holocentroides moldavicus*, while the forms previously determined to the level of genus as *Africentrum* represented in fact this one species only. Therefore, lists of taxa published in the above papers contain neither *Africentrum* nor *Holocentroides* taxa. Unfortunately, this change of name has not been marked on numerous name tags of *Africentrum* specimens. Hence, observing the rule of exact representation of the state of the collection, its description maintains the names of both generic taxa and the affinity of *Africentrum* to family Trachyichthyidae, earlier suggested by A. Jerzmańska (Jerzmańska & Kotlarczyk, 1975). However, taking into account that the creator of *H. moldavicus* considered it closely similar to recent *Holocentrus* (Paučá, 1931, 1933), and that Arambourg (1927), the creator of *Microcentrum* taxon, later renamed as *Africentrum* (White & Moy – Thomas, 1941), assigned his new genus to family *Holocentridae*, it can be accepted that specimens of *Africentrum* derived from FishCarpathZPAL/WR collection do also represent this family. The same systematic position was suggested by Nelson (1994). These comments should help in understanding the apparent discrepancy in assigning *Africentrum* specimens once to Trachyichthyidae, and another time to Holocentridae families.

Returning to the origin of the IPM5 Zone assemblage, it is worth to note that the entire family Holocentridae, including also fossil taxa (Bannikov & Parin, 1997), is associated with a biotope of coral reefs. Therefore, a large share of representatives of this family in the zonal assemblage (27.4%; cf. Figs 26, 30, 31) is difficult to understand and provides a research challenge. These two formally considered taxa provide only a background to a few other zones of UBA; hence, their mass occurrence in the IPM5 Zone only is a particularly striking feature. Taking into account a deep-water character of one-third of fish in this assemblage, it would be difficult to explain solely by a reflection of *acme* event of these shallow-water form(s).

An analysis of this feature should be aided by a review of the behaviour of other taxa during the existence of UBA

in the Menilite basin. Figure 32 shows groups of taxa that are characterised by comparable shape of curves representing the percentage of each taxon in zonal assemblages, irrespectively of their affinity to different ecological environments.

Genera representing the same biotope, although differing by the shape of curves, have also been classified into groups. The diagram clearly shows that culminations similar to those of the two discussed taxa refer also to benthopelagic: *Zeus* and *Lepidopus*, demersal: *Scorpaenoides* and, to a smaller degree, *Serranus*, and even epipelagic: *Clupea* and *Palaeorhynchus* taxa. These are negatively correlated with *Eomyctophum* and less clearly with *Vinciguerrria*. A rapid decrease in the share of *Eomyctophum* is notable: from a high amount in zones IPM4, IPM6, and IPM7 to the level observed in Zone IPM4A.

All these facts should have had one common origin. However, the latter can be associated neither with a basin shallowing, due to the presence of MB taxa, nor with filling of the basin by gases preventing the development of life, due to the occurrence of abundant deep-water, benthopelagic fishes. The last fact, together with coeval decrease in the *Eomyctophum* population, implies that the latter could have been induced by formation of the anaerobic layer, although in a higher part of the water column only. This hypothesis does not explain, however, a large proportion of fishes representing the neritic-reefal environments within the tanathocoenosis. Within assemblages of other deep-water zones, this proportion does not exceed ca. 6% (attaining maximum values in zones IPM1, IPM4A, and IPM4).

It seems likely that the proper origin of formation of the IPM5 Zone assemblage has been identified.

The IPM5 Zone assemblage was found a few tens of metres above JLH, i.e. most probably still within the upper part of a nannoplankton biozone NP24, whose boundaries were dated by Berggren *et al.* (1995) at 27.6 Ma and 30 Ma, respectively. In this biozone, at the boundary between the Chattian and Rupelian, dated by Berggren *et al.* (1995) at 28.5 Ma and by Gradstein *et al.* (2004) at 28.4±0.1 Ma, the greatest Palaeogene glaciostatic sea level fall occurred, amounting to ca. 175 m (Haq *et al.*, 1988) (Fig. 33). Nearly the entire shelf bottom was exposed and the biotope of near-shore fish became restricted to a narrow zone close to the shelf break. The dying fishes could have been easily transported in large quantities above the slope towards the continental rise and axial parts of the trench. The sea level fall lasted with some interruptions until the onset of the Miocene.

This situation resulted not only in shaping of an atypical assemblage of the IPM5 Zone, but also decisively controlled the type and composition of assemblages of younger zones which developed throughout NP25 – NN1 (?) biozones. There occurred a decrease in percentage of benthopelagic fishes dwelling the upper part of the slope (*Lepidopus*), being accompanied by an increase in fish penetrating greater depths (*Merluccius*, *Palaeogadus*) (Fig. 32). First of all, a rapid increase in the share of *Syngnathus*, followed by equally rapid increase in the number of thalli of brown algae, was observed. In the latter, there occurred genera bearing specifically branching thalli and air bladders

which are characteristic for genus *Sargassum*. This finding led Jerzmańska and Kotlarczyk (1975) to distinguish a quasi-Sargasso assemblage within Zone IPM6, being ecologically similar to an assemblage which can presently form at the bottom of the Sea of Sargasso. In a fossil tanathocoenosis, this assemblage is composed of meso-bathypelagic fishes, like: *Eomyctophum*, *Idrissia*, *Vinciguerrria*, *Argyropelecus*, and others; shallow-water, littoral genera, and pelagic forms: *Syngnathus*, *Ammodytes*, and *Lepidopus isopleurus* of a very elongated body, probably adapted to dwelling among algae; *Clupea* and others. It is worth to add that the structure of armoring plates and the pattern of pointed spine on the bodies of fossil specimens of *Syngnathus incompletus* are largely similar to those of a recent species *Syngnathus pelagicus*, which dwells among algae of the Sea of Sargasso (Dolińska, in: Jerzmańska & Kotlarczyk, 1975).

It can be concluded from the described assemblage composition that the hardly interpretable origin of the specialised, recent Sargasso assemblage can only be explained when turning back to the very beginning of the latter, i.e. Oligocene time in the Western Tethys (Carpathians - Caucasus), migration of the assemblage to the Western Atlantic, and its further evolution therein (Jerzmańska & Kotlarczyk, 1976).

It deems necessary to recall in this place the discovery of typical *Sargassum* algae in slightly younger strata in the foreland of Caucasus. The *Sargassum maicopicum* thalli, found in sediments of the Upper Maikop Beds (Zuramakent Horizon, Burdigalian), were described by a botanist named Polibin, in 1941 (*vide* Hecker & Merklin, 1946). The accompanying fish assemblage was composed of mass-occurring *Sardinella*, numerous *Merluccius*, and other species. These components resemble, from the ecological point of view, those comprised in the INM1 Zone assemblage in the Carpathians.

The above hypothesis of the origin of the Sargasso Sea assemblage is firmly confirmed by the reconstructed causes that led to formation of the IPM5 Zone tanathocoenosis. Namely, emergence of the nearly entire shelf bottom ca. 28.5 Ma resulted also in destruction of the algal biotope and fostered its adaptation to dwelling in pelagial waters. This gave rise to a long-term evolution of the Sargasso assemblage.

As shown above, each assemblage of the zones of the second pattern was of different origin. The IPM4A Zone assemblage was formed on a peculiar morphological element of the basin, i.e. the slope of a submarine ridge, while the two remaining assemblages originated due to changes of environmental conditions that affected the entire basin.

SUMMARY AND CONCLUDING REMARKS

1. A very important task of this study was to organize, conservate, document and electronically catalogue a collection of fossil Carpathian fishes housed at the Department of Palaeozoology of the Institute of Zoology, University of

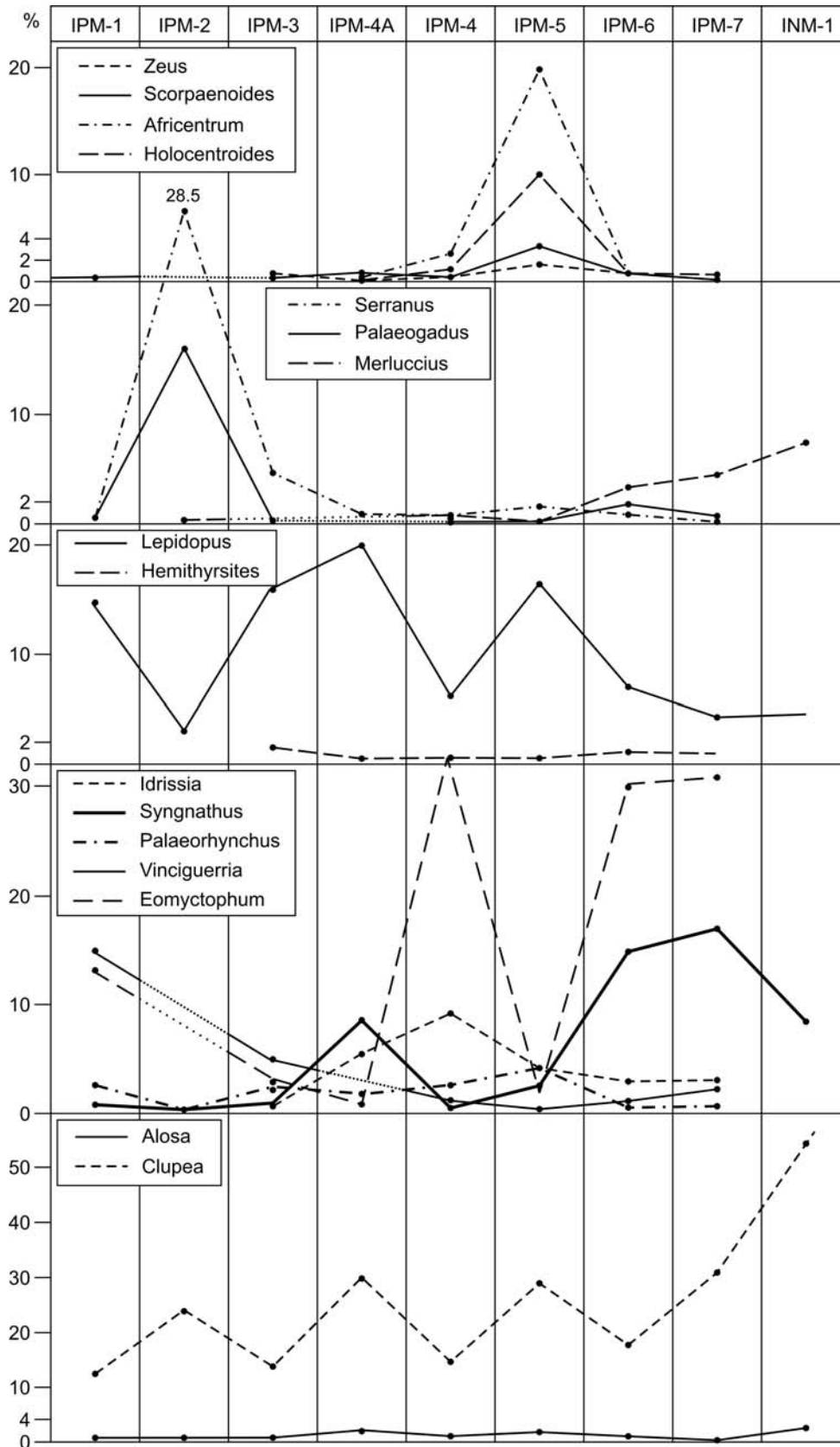


Fig. 32. Time-series graphs showing percentage of selected fish genera within assemblages of zonal taphocoenoses of Oligocene–Early Miocene age in the Polish Carpathians

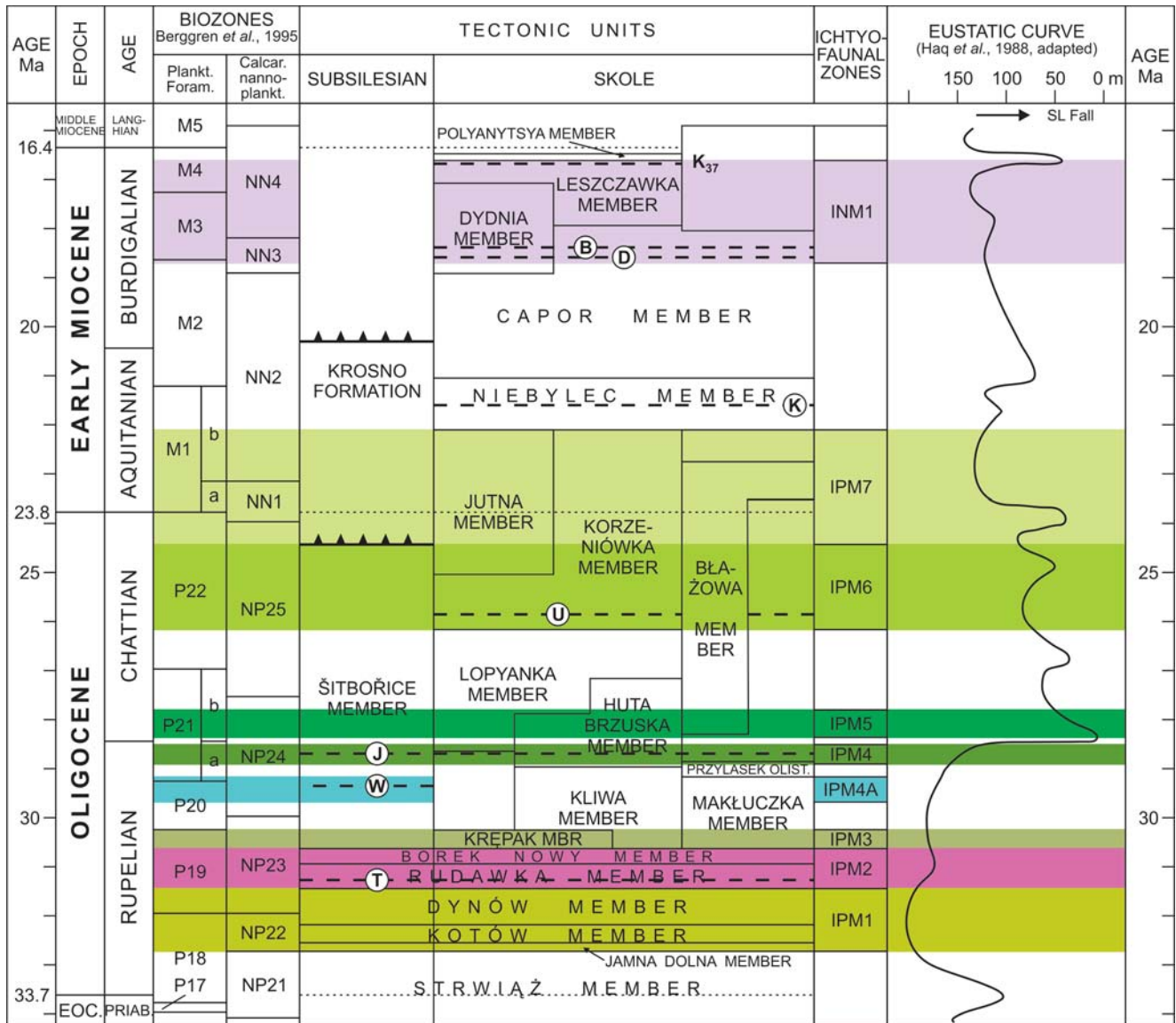


Fig. 33. Correlation of ichthyofaunal zones with litho-, bio-, and chronostratigraphy of the Menilite-Krosno Series in the Skole and Sub-silesian units of the Polish Carpathians (compiled by J. Kotlarczyk, this paper). Marker horizons as on Fig. 2. Bathypelagical assemblages were distinguished by green and neritic – sublitoral ones by violet colours

Wrocław, completed in the years of 1958–1996. The collection numbers ca. 13,000 specimens, including: 3,314 complete skeletons, 6,382 incomplete skeletons, 1,583 fish heads, and other remains. After verification of ca. 9,000 specimens undescribed in publications, and taking into account published data pertaining to ca. 4,000 specimens, systematic composition of the collection was established. Division Teleostei includes representatives of 21 orders (plus 1 indet.), 55 families (plus 19 indet. and 2 *incertae sedis*), and 73 genera (plus 64 indet.). As far as the basic taxonomic level is concerned, 61 species were distinguished. Classis Chondrichthyes bears representatives of 3 genera, 3 families, 2 orders, and 1 Subclassis.

The state of description is not fully satisfactory. From ca. 12,930 specimens of Teleostei, ca. 10,640 specimens were identified to the level of genus (and – to a lesser degree – species), while to higher-ranking taxonomic units ca.

1,600 specimens were identified. In case of ca. 450 specimens, even identification to the level of order was not possible. Another group consisted of ca. 250 specimens which were not included in this study due to doubts expressed by the identifying palaeontologist, Prof. A. Jerzmańska, who maintained question marks marked in archival labels. In general, the share of specimens of Teleostei that require further study to obtain data at least at the level of genus, amounts to 18% of the total.

Nevertheless, further revisions of the already identified taxa deem necessary. This is indicated by recent findings within the collection of the *Anencheleum* and *Horbatshia* taxa, as well as the results of a revision of a few Caucasian taxa, identified by A. Jerzmańska in the Carpathian collection. According to the results of osteological analysis by Prokofiev (2002b), *Vinciguerria obscura* and *V. talgiensis* belong to the newly-created genus *Eovinciguerria* gen.nov.,

whereas *V. distincta* – to the new taxon *Sychevskia* gen. nov.

The Carpathian fish collection, organized and made available to scholars, will certainly contribute to the progress in palaeoichthyology.

2. The Carpathian fish collection was assembled at 222 exposures. Nearly half of them (118) contained up to 10 specimens, whereas 28 exposures provided more than 100 specimens. It was possible to re-identify in the field most of the exposures, completing their missing lithological descriptions. Altogether, 1,170 m of the geological section was fully documented, compared to min. 1,370 m of palaeontologically sampled section (some of exposures were destroyed). Numerous exposures enabled identification of the exploited fauna-bearing layers, whereas at the remaining ones only the extent of sampled fragments could be detected. Ichthyofaunal assemblages of the latter fragments were ecologically homogeneous.

3. The identified, sampled exposures were linked with stratigraphic logs of the Menilite-Krosno Series. The latter were reconstructed for either single, complete cross-sections through an outcrop of MKS, or as synthetic sections combining a few neighbouring partial sections.

In the eastern part of the Polish Carpathians, 18 sections were reconstructed to portray the arrangement of successive structures from the inner to outer parts of the flysch Carpathians. These structures represent the following tectonic units: Dukla – 1 section, Silesian – 3 sections, Subsilesian – 2 sections, Skole – 10 sections, and Boryslav-Pokuttya – 2 sections. In the Western Carpathians, in turn, 2 sections associated with the outer units were reconstructed. Marker horizons, such as: the Tylawa Limestone (TL), Wujskie Limestone (WL), Jasło Limestone (JL), the V Tuff Horizon, the Piątkowa Diatomite Horizon (dP) and others helped to correlate individual sections and to link the exposures with their respective lithostratigraphic members.

For the purpose of this study, the lithostratigraphic scheme of the Menilite-Krosno Series was supplemented, and basing on new published data an attempt of correlating the distinguished lithostratigraphic units with calcareous nannoplankton biozones (NP22 to NN4; Fig.2) was made. In addition, it was excluded that the highest strata of the MKS would represent ages younger than the early Carpathian.

It was also shown that the radiometrically dated Radziszów Tuff is not equivalent to the V Tuff Horizon (Sikora *et al.*, 1959), for which the name Dobrzanka Tuff was proposed.

4. A model of sedimentation of the Menilite Formation in the eastern Carpathian basin of Poland was reconstructed. The basin infilling was linked with the activity of submarine fans which supplied clastic material both from the northern land (Menilite facies) and from the south-east (Krosno facies of the Lopyanka and Jutna members).

Fossil fishes were found mainly in sediments of the E.2.2, E.2.1, and G.1.2, sometimes E.1.2 and G.2.1 facies of Pickering *et al.* (1986), usually within parallel laminated sediments. Reconstruction of the sedimentary basin enables one to pinpoint places of burial of individual ichthyofaunal assemblages and to reconstruct some of mechanisms

and *post mortem* transport routes of fish bodies. It was found out that most of the exploited ichthyofaunal assemblages were formed at the bottoms of the Silesian and Skole troughs and on the continental rise of the latter, and – to a lesser degree – on the continental slope (Boryslav-Pokuttya Unit) and both slopes of the Sanok submarine high (Subsilesian Unit).

5. The collected abundant ichthyofaunal material made it possible, in the first step of the analysis, to investigate the range of variability of assemblages of ichthyofaunal assemblages in the stratigraphic log, and their lateral variability within defined time slices. This analysis concerned only those exposures whose stratigraphic position was well constrained.

Analysis of assemblage variability at the lowest possible level, i.e. between neighbouring layers, helped to document – at a dozen or so exposures – the position of sharp boundaries between different ecological assemblages and between assemblages bearing different spectra of taxa within the distinguished ecological assemblages. Similar boundaries were identified all over the study area when analyzing variability of ichthyofaunal assemblages among exposures of individual stratigraphic sections. Taking into account hiatuses occurring sometimes in the sampled single sections, composite sections based on several neighbouring synthetic sections were constructed.

This type of analysis helped to indicate taxa dwelling the basin throughout its existence (ca. 16 m.y.), as well as those which either appeared or disappeared from the basin in different times. These appearances and disappearances usually reflect ecological changes of the environment, and also result from the migration of taxa along the northern Tethys margin. The first and last appearances of taxa in the study area are marked by acronyms: F_{EAD} and L_{EAD}. Mass occurrences of single taxa or their assemblages numbering few elements, restricted to single layers or narrow section fragments, were also identified. These occurrences reflect such events, as periodical mass reproductiveness or, more probably, mass mortality.

Analysis of lateral variability of assemblages among exposures of the Jasło Limestone chronohorizon or exposures of thin members, such as the Kotów Chert or Dynów Marl members, points to a much lesser variability, although noticeable is the lack in some exposures of some usually abundant taxa, or step-like increases in the number of specimens of the given taxa in other exposures of the same horizon. These changes appear to indicate local variability of ichthyofaunal assemblages.

The analyses of vertical and lateral ichthyofaunal variability show without doubt that the observed variability can largely result from small representativeness of sampling of individual layers or exposures. This calls for great caution in interpreting the origin of variability.

6. Previous studies, based on a collection numbering ca. 4,000 specimens, resulted in a subdivision of the MKS into 7 ichthyofaunal zones (Kotlarczyk & Jerzmańska, 1988a). Further analysis aimed at extending and more precise determination of this zonation, taking into account abundant material gathered from the Subsilesian Unit and from previously unstudied segments of the MKS section comprised between ichthyofaunal zones within the upper bathypelagic assemblage.

As a result, a new zone in the Subsilesian Unit was distinguished, i.e. the IPM4A Zone that overlies the simultaneously distinguished Wujskie horizon of laminated limestones. Moreover, a new zone IPM7 was distinguished in the top part of the Menilite Formation of the Skole Unit. In addition, new subzones in the lower part of the Miocene zone and the lower part of the IPM2 Zone were defined.

It was also shown that between the IPM3, IPM4A, IPM4, IPM5 and IPM6 zonal assemblages there occurred uncharacteristic meso-bathypelagic assemblages, devoid of either index or representative taxa. The IPM7 and INM1 zones, in turn, are separated by a barren interzone.

7. One of principal tasks of this study was to determine temporal extents of individual taxa, and to reconstruct the complete composition of zonal taxa. This task was fulfilled basing on exposures bearing representative taxa, and those devoid of such taxa but of well-constrained stratigraphic position.

The number of specimens of individual zonal assemblages changes between ca. 450 to 3,280 (IPM6), identified to the level of either species or genus. In the majority of zones, the number of taxa is constant and usually independent of the number of specimens. The former averages at 40, increasing to 66 in the IPM6 Zone and falling to 29 in the IPM7 Zone. The number of representative and index taxa ranges between 4 and 11, except for the IPM7 Zone which does not have any taxon (leaving aside one shark) occurring exclusively in this zone. In the least documented INM1 Zone (150 specimens), the number of taxa is proportionally lower (11), although representative taxa fall within the interval typical for other zones. Changes in the number of individual taxa within the zones and their ranges, illustrating the variability of 9 zonal assemblages, are synthetically portrayed in Table 25 which is of crucial importance for drawing ecostratigraphic conclusions.

A single, short-lived (from a few hundred thousand to less than two million years) appearance in the basin of taxa occurring exclusively in a given zone usually points to migratory character of such assemblages. This is also indicated by high specialization of some taxa (e.g. *Argyropelecus*), which must have been formed outside the Carpathian basin, i.e. in the Indo-Pacific Ocean (cf. Jerzmańska & Kotlarczyk, 1981) and, in some cases, in the Atlantic. Disappearance of some taxa could have also been associated with their extinction (e.g., *Eovinciguerrria talgiensis* (Dan.) – zone 1, *Eophycis jammensis* Jerz. – zone 2) or a drastic change of environmental conditions (e.g., *Scopeloides* sp. – zone1).

8. An analysis of succession of ichthyofaunal assemblages enabled for correction of the previous zonation and for a new formal description of the distinguished ecostratigraphic zones and subzones. The zones IPM4A and IPM7 were defined, and the remaining ones were re-defined. Three zones represent taxon-range zones (IPM4, IPM5, IPM6), three are assemblage zones (IPM1, IPM4A, INM1), two represent concurrent range zones (IPM2, IPM3), and one (IPM7) – successive last appearance zone.

Two subzones (IPM2-T.SUB. and INM-L.SUB.) were defined, and one subzone (IPM1-C.SUB.) was redefined. Due to the lack of data pertaining to temporal extent of epiboles of *Syngnathus incompletus*, the IPM6-S was not re-

defined. Both zonal and boundary stratotypes were determined for all distinguished zones and subzones.

The collected material enabled us to distinguish mass occurrences of the taxon *Centriscus* as: 1st *Centriscus* event in the Early Rupelian (ca. 32.5 Ma) and the 2nd *Centriscus* event in the Late Rupelian (ca. 29.3 Ma).

The IPM1, IPM2 and IPM4 zones are widespread throughout the study area. In the Silesian Unit no assemblages of the zones IPM3, IPM5, IPM6 and IPM7 were found, except for single specimens representing the upper bathypelagic assemblage (Łodygowice). It means that there were no suitable conditions for burial and preservation of dead fish bodies. The Silesian and Subsilesian units bear no fishes of the INM1 Zone due to the lack of sediments of such an age. The IPM4A Zone assemblage is restricted to the Subsilesian Unit and, in traces, to the Boryslav-Pokuttya Unit. This restriction is associated with specific ecological conditions of the basin slopes. A slightly smaller extent of zones 3 and 5 compared to zones 4, 6, and 7 in the Skole Unit probably results from sedimentary facies of these zones, not suitable for preservation of ichthyo-tanathocoenoses (oxidized sandstones and shales), and partly from less intensive exploration of assemblages of these zones.

9. Palaeoecological analysis, using data pertaining to environmental conditions of taxa living today or those closest to extinct taxa, helped to distinguish in the fossil material several ecological groups of ichthyofauna. These include: the epipelagic (EP), mesopelagic (MP), bathypelagic (BP), benthopelagic (BEP), demersal and bathydemersal (D + BD), neritic (N) and reefal (R) groups.

In this respect, assemblages of the distinguished 9 zones were characterised. It was found out that: (1) the EP and BEP fishes maintain a large share in all these assemblages; (2) the MP and BP fishes are numerous in the IPM1, IPM3, IPM4, IPM6 and IPM7 zones only; (3) the D+BD fishes make up important proportion in the IPM2 and IPM4A zones only; and (4) fishes of the N+R group are important solely in the IPM5 Zone.

Taking into account proportions of all ecological groups within zonal assemblages, three patterns of zonal composition can be observed. The first pattern occurs in those zones where the EP+MP+BP fishes decisively dominate over the BEP+D+BD+N+R ones; these zones were mentioned above in paragraph (2). The second pattern is characterised by a reverse proportion of these groups and occurs in zones IPM2, IPM4A and IPM5. The third pattern occurs in the INM1 Zone only, where the EP and BEP fishes occur, the share of the former being 2.5 times greater.

10. The formation of so different ichthyofaunal assemblages resulted, first of all, from different factors affecting their ecological environment, the rate of fish evolution, migration of new taxa, and configuration of the basin bottom.

Assemblages of the **first pattern** were formed throughout the entire Oligocene. The ichthyofaunal composition points to a relatively deep basin, exceeding a depth of 2,000 m. Ubiquitous occurrence of the EP-MP-BP fishes within tanathocoenoses is fully understandable. These fishes represent an autochthonous element. Likewise, widespread occurrence of the BEP fishes dwelling waters down to a depth of 400–500 m (sometimes even 1,000 m), and

D+BD fishes dwelling down to 200 m and sometimes 500 m depths, as well as neritic and reefal fishes testifies to intense and rapid *post mortem* transport. All these fishes represent an allochthonous element of the tanathocoenosis.

The origin of the assemblage of the **third pattern** at the end of deposition in the Skole basin, devoid of MP and BP forms but rich in taxa tolerating brackish conditions, could have resulted from a marked basin shallowing due to its filling by ca. 1 km thick pile of sediments.

To explain the origin of assemblages of the **second pattern** requires separate description of each of the three cases. A large share of all ecological groups in the IPM4A Zone assemblage can be well explained by the formation of a tanathocoenosis on the slope of a submarine ridge, dwelled by fishes of the thalasso-benthopelagial, and where to fishes derived from the thalasso-epibenthal and thalasso-epipelagial could have easily been transported.

The most difficult task is to reconstruct the origin of IPM2 Zone. A previous concept explaining elimination of MP and BP fishes from the basin by a lowering of water level in a dessication basin appears to be less probable as compared to an option maintaining that the northern Tethys basin was periodically characterised by anaerobic conditions. The lack of oxygen resulting from a high TOC content in sediments, existing nearly throughout deposition of the Menilite Formation, was noticeable in the studied time interval in the lower water column, up to an isobath of 500 m. This situation helped to survive shelf-dwelling taxa, as well as those associated with the shelf break and upper part of slope, but forced elimination of deep-water fishes. The mechanism of distribution of shallow-water taxa all over the basin bottom probably resembled that of the already described assemblages of the first pattern. An allochthonous character of the IPM2 tanathocoenoses appears to be indicated by smaller proportions of fossil fishes exploited from 1 m of section of this zone, compared to analogous proportions of sections of bathypelagic zones, as well as by the occurrence of a layer rich in specimens of shallow-water taxa (Trachinus event) in the middle of the basin. The appearance of oxygen minimum in the basin can be associated with a rapid decrease in the influx of oxygenated waters from the ocean via the Rhine Graben and Slovenian Corridor (SC), probably induced by a sea level fall at ca. 31.5 Ma.

The greatest Palaeogene glaciostatic sea level fall of 175 m, dated to ca. 28.5 Ma (Haq *et al.*, 1988), was in turn responsible for the formation of the IPM5 Zone assemblage. The N and R (and also D) fish biocoenoses, shifted towards the shelf break, could have easily supplied tanathocoenoses of the continental slope and rise. In this manner, assemblages rich in deep-water taxa (Alepocephalidae) could have been supplemented by a component typical of shallow-water environments. On the other hand, the presence of very deep-water forms of benthopelagic fishes implies a good connection between the Carpathian basin and open ocean. This connection was not affected by the above-mentioned sea level fall.

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Streszczenie

**PODSTAWY EKOSTRATYGRAFII
ICHTIOFAUNISTYCZNEJ OSADÓW
OLIGOCENU–WCZESNEGO MIOCENU BASENU
ZEWNĘTRZNYCH KARPAT POLSKICH**

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1. Jako bardzo ważny rezultat przeprowadzonych prac należy uznać uporządkowanie, zakonserwowanie, udokumentowanie i skatalogowanie [na nośnikach elektronicznych] karpackiej kolekcji ryb Zakładu Paleozoologii Instytutu Zoologicznego, kompletowanej w latach 1958 – 1996. Liczy ona ok. 13000 okazów, w tym 3314 kompletnych szkieletów, 6382 – niekompletne szkielety, 1583 głowy i inne szczątki (Tab. 3). Po przeprowadzeniu weryfikacji oznaczeń ok. 9000 okazów nie opisanych w publikacjach i uwzględnieniu danych publikowanych, dotyczących ok. 4000 okazów, ustalono skład systematyczny kolekcji. Dział Teleostei reprezentują przedstawiciele 21 rzędów (plus 1 indet), 55 rodzin (plus 19 indet. i 2 *incertae sedis*) oraz 73 rodzaje (plus 64 indet.). Na podstawowym poziomie taksonomicznym wyróżniono w kolekcji 61 gatunków. Gromadę Chondrichthyes reprezentują przedstawiciele 3 rodzajów, 3 rodzin, 2 rzędów i 1 podgromada.

Stan opracowania kolekcji należy uznać za niezbyt zadowalający. Na ok. 12930 okazów Teleostei do poziomu rodzaju (i w mniejszym stopniu – gatunku) oznaczono ok. 10640 osobników, do wyższych jednostek taksonomicznych – ok. 1600 okazów. W przypadku ok. 450 okazów nie udało się zidentyfikować ich przynależności nawet do rzędu. Odrębną grupę stanowi ok. 250 okazów, nie uwzględnionych w opracowaniu, z uwagi na wątpliwość oznaczającego paleontologa, wyrażoną znakiem zapytania pozostawionym przez prof. A. Jerzmańską na metryczkach archiwalnych. Ogółem można powiedzieć, że udział okazów Teleostei wymagających dalszego opracowania, celem uzyskania danych przynajmniej na poziomie rodzaju, wynosi ok. 18% składu kolekcji.

Niezależnie od powyższego, konieczne będą dalsze rewizje wyznaczonych już taksonów. Wskazuje na to, ujawniona w ostatnich latach, obecność w zbiorze taksonów *Anencheleum* i *Horbatshia* a także rezultaty rewizji kilku taksonów kaukaskich, wyróżnionych w kolekcji karpackiej przez A. Jerzmańską. Na podstawie analizy osteologicznej Prokofiev (2002b) wykazał, że taksony *Vinciguerria obscura* i *V. talgiensis* należą do nowokreowanego rodzaju *Eovinciguerria* gen. nov., zaś *V. distincta* podobnie do nowego taksonu *Sytchevskia* gen. nov.

Uporządkowana i udostępniona badaczom kolekcja karpacka przyczyni się, jak mamy nadzieję, do postępu prac w zakresie paleoichtiologii kenozoiku.

2. Kolekcja karpacka została zebrana w 222 odkrywkach (Tab. 1, Fig. 1, reprezentujących głównie formację menilitową, w niewielkiej części formację krośnieńską). W około połowie (118) odkrywek ilość 4. egzemplarzy nie przekraczała 10; więcej niż 100 egzemplarzy zebrano w 28 odkrywkach. Zdecydowaną większość odkrywek udało się zidentyfikować ponownie w terenie i sporządzić brakujące dokumentacje litologiczne. Łącznie udokumentowano 1170 m zapisu geologicznego, na minimum 1370 m opróbowanego paleontologicznie profilu (część odkrywek uległa destrukcji). W dużej ilości odkrywek udało się zidentyfikować położenie eksploatowanych warstewek z fauną, w pozostałych jedynie zasięg opróbowanych fragmentów profilu (Fig. 6). W tych ostatnich zebrane zespoły ichtiofauny były jednorodne pod względem ekologicznym.

3. Zidentyfikowane, opróbowane odkrywki powiązano z profilami stratygraficznymi serii menilitowo-krośnieńskiej (Fig. 3–5). Te ostatnie zrekonstruowano bądź dla pojedynczych kompletnych przekrojów przez wychodnię MKS (serii menilitowo-krośnieńskiej), bądź jako profile syntetyczne, złożone z kilku sąsiednich profili cząstkowych. W przypadkach, gdy materiał paleontologiczny w profilach syntetycznych był dość skąpy, konstruowano na podstawie kilku sąsiednich profili i dodatkowych rozproszonych odkrywek profile zbiorcze, reprezentujące większe fragmenty (strefy) badanej powierzchni basenu (Fig. 9).

We wschodniej części Karpat polskich zrekonstruowano 18 profili dających przekrój przez struktury uszeregowane od wnętrza Karpat ku ich brzegowi. Reprezentują one kolejne jednostki tektoniczne: dukielską – 1, śląską – 3, podśląską – 2, skolską – 10, borysławsko-pokucką – 2 profile. W Karpatach zachodnich zrekonstruowano 2 profile, związane z jednostkami zewnętrznymi. Horyzonty przewodnie: wapienie z Tylawy (TL), wapienie z Wujskiego (WZ), wapienie z Jasła (JL), tuf z horyzontu V, poziom diatomitów z Piątkowej (dP) i inne ułatwiły korelacje profili i powiązanie odkrywek z ogniwami litostratygraficznymi (Fig. 3, 4).

Dla potrzeb opracowania uzupełniono schemat litostratygrafii MKS, a w oparciu o dane literaturowe przeprowadzono próbę powiązania wyróżnionych jednostek litostratygraficznych z biozonami nannoplanktonu wapiennego – od NP22 po NN4 (Fig. 2). Wykluczono przy tym możliwość datowania najwyższych warstw w profilu MKS na wiek młodszy niż dolny karpac.

W wyniku przeprowadzonej dyskusji zanegowano możliwość identyfikacji tufu z Radziszowa, datowanego radiometrycznie, z tufem poz. V (Sikora *et al.*, 1959), dla którego wprowadzono nazwę tufu z Dobrzanki (Tab. 2).

4. Zrekonstruowano model sedymentacji formacji menilitowej w basenie wschodniej części Karpat polskich (Fig. 7), wiążąc zasypywanie basenu z działalnością stożków podmorskich, dostarczających materiał klastyczny z lądu północnego (facja menilitowa) bądź od strony SE (facja krośnieńska w ogniwach z Łopianki i z Jutnej) (Fig. 8).

Stwierdzono występowanie ryb kopalnych głównie w osadach facji E.2.2, E.2.1, G.1.2, niekiedy w osadach facji E.1.2 i G.2.1 Pickeringa *et al.* (1986), przeważnie (choć nie tylko) w osadach laminowanych płasko-równoległe (Fig. 6).

Rekonstrukcja basenu sedymentacyjnego pozwala na zdefiniowanie miejsc pogrzebienia poszczególnych ichtiotanocenozy i odtworzenie niektórych mechanizmów i dróg transportu pośmiertnego ciał ryb. Ustalono, że zdecydowana większość eksploatowanych tanocenozy utworzyła się na dnach rynny śląskiej i rynny skolskiej oraz na podniesieniu kontynentalnym tej ostatniej, a w mniejszym stopniu na skłonie kontynentalnym (jednostka borysławsko-pokucka) i obu skłonach sanockiego wyniesienia podmorskiego (jednostka podśląska) (Fig. 7).

5. Zebrany obfity materiał ichtiofaunistyczny pozwolił w pierwszym kroku analizy na zbadanie zakresu zmienności zespołów tanocenozy, zarówno w profilu stratygraficznym, jak i zmienności lateralnej wewnątrz określonych poziomów czasowych. W rozważaniach uwzględniono tylko te odkrywki, których pozycja w profilu została dobrze określona.

Analiza zmienności zespołów na najniższym możliwym poziomie, tj. między sąsiednimi warstewkami pozwoliła na udokumentowanie w kilkunastu odkrywkach (Tab. 4–10) położenia ostrych granic między różnymi zespołami ekologicznymi, bądź zespołami zawierającymi różne spektra taksonów w obrębie wyróżnionych zespołów ekologicznych. Podobne granice zostały wykryte na całym obszarze badań podczas analizy zmienności zespołów ichtiofauny między odkrywkami w poszczególnych profilach stratygraficznych. Z uwagi na występujące niekiedy luki w opróbowaniu pojedynczych profili, konstruowano profile zbiorcze na podstawie kilku sąsiednich profili syntetycznych (Tab. 11–19).

Ten rodzaj analizy pozwolił na wskazanie taksonów żyjących w basenie w całym okresie (ok. 16 mln lat) jego trwania, a także tych, które pojawiły się w nim bądź znikły w różnych momentach czasowych. Te pojawienia się i zaniki są przeważnie odzwierciedleniem zmian ekologicznych w środowisku a także rezultatem migracji taksonów wzdłuż północnego basenu Tetydy. Dla tego typu pierwszych i ostatnich wystąpień taksonów na badanym obszarze zastosowano akronimy: F_{EAD} i L_{EAD} . Wykryto także wystąpienia masowych nagromadzeń pojedynczych taksonów lub ich kilkuelementowych zespołów, ograniczonych do pojedynczych warstewek lub wąskich odcinków profilu (Tab. 4, 6). Są one przejawem takich zdarzeń, jak czasowa gwałtowna rozrodczość bądź, co bardziej prawdopodobne, masowa śmiertelność.

Analiza lateralnej zmienności zespołów między odkrywkami chronohoryzontu wapieni jasielskich (Tab. 20) lub odkrywkami cienkich ogniw, typu rogowców z Kotowa, czy margli z Dynowa (Tab. 21) wykazała znacznie mniejszą zmienność, choć znamienne są braki w jednych odkrywkach niektórych, zwykle licznie pojawiających się taksonów, bądź skokowe przyrosty ilości osobników danych taksonów w innych odkrywkach tego samego poziomu. Zdają się one świadczyć o lokalnej zmienności ichtiocenozy. W przypadku porównywania zespołów pochodzących z odkrywek grubszego pakietu łupków menilitowych (Tab. 22), obserwowane podobne lateralne zmiany składu ryb mogą dodatkowo wynikać z porównywania składu ichtiofauny zebranej z warstw różniących się nieco wiekiem. W tych sytuacjach pozorna zmienność lateralna byłaby odbiciem zmienności wertykalnej tanocenozy.

Analiza pionowej i lateralnej zmienności ichtiofauny wykazała ponadto niezbicie, iż obserwowana zmienność może w znacznej mierze wynikać z małej reprezentatywności opróbowania poszczególnych warstewek lub odkrywek. Nakazuje to dużą ostrożność w interpretacji przyczyn zmienności.

6. Wcześniej opracowania oparte o zbiór liczący ok. 4000 egzemplarzy przyniosły podział MKS na 6 zon (Fig. 10) a następnie na 7 zon ichtiofaunistycznych (Kotlarczyk & Jerzmańska 1988a). Kolejny krok niniejszej analizy zmienności ichtiofauny zmierzał do poszerzenia i uściślenia tej zonacji. Przesłanką do tego było zebranie obfitego materiału w jednostce podśląskiej, a także w niezbadanych wcześniej odcinkach profilu MKS, występują-

cych między zonami ichtiofaunistycznymi w obrębie górnego zespołu batypelagicznego (Fig. 14–19).

Efektom tego etapu analizy zmienności było uściślenie składu i zmienności zespołu ryb zony IPM5 (Fig. 11) oraz uzasadnienie wyodrębnienia w jednostce podśląskiej nowej zony IPM4A (Tab. 23 i Fig. 12), występującej nad równocześnie wyróżnionym poziomem wapieni laminowanych z Wujskiego, a także uzasadnienie wyodrębnienia nowej zony IPM7 w stropowej części formacji menilitowej jednostki skolskiej (Fig. 20).

Ponadto wyodrębniono nowe podzony w obrębie dolnej części zony mioceńskiej i dolnej części zony IPM2.

Wykazano także, iż między zespołami zonalnymi IPM3, IPM4A, IPM4, IPM5 i IPM6 występują niecharakterystyczne zespoły mezo-batypelagiczne pozbawione taksonów indeksowych bądź reprezentatywnych. Przykładem takiego zespołu jest skład ryb (Fig. 13), pojawiający się w odkrywkach występujących powyżej poziomu wapieni jasielskich, typowany wstępnie w analizie do wyodrębnienia nowej zony IPM4B. Zony IPM7 i INM1 rozdziela natomiast międzyzona jałowa (Fig. 20).

7. Jednym z głównych celów opracowania było ustalenie zasięgów czasowych poszczególnych taksonów a także określenie pełnego składu taksonów zonalnych. Dokonano tego w oparciu o odkrywki zawierające taksony reprezentatywne, a także o odkrywki ich pozbawione ale posiadające dobrze określoną pozycję stratygraficzną (odkrywki podstawowe zestawiono na Tab. 24).

Liczebność poszczególnych zespołów zonalnych waha się od ok. 450 do ok. 3280 (IPM6) egzemplarzy oznaczonych do poziomu gatunku lub rodzaju. Liczba taksonów jest w większości zón stała, w zasadzie niezależna od ilości egzemplarzy i waha się ok. 40, jedynie w zonie IPM6 ilość ta wzrosła do 66 a w zonie IPM7 jest trochę niższa – 29 egz. Ilość taksonów reprezentatywnych, łącznie z indeksowymi waha się od 4 do 11. Wyjątek stanowi zona IPM7, która nie posiada żadnego taksonu (poza 1 rekinem) występującego wyłącznie w tej zonie. W najmniej udokumentowanej zonie INM1 (150 egz.) ilość taksonów jest odnośnie niższa (11), choć ilość taksonów reprezentatywnych mieści się w podanym wyżej przedziale dla innych zón. Zmiany liczebności poszczególnych taksonów w zonach i ich zasięg, ilustrujące zmienność 9 zespołów zonalnych, syntetycznie ujęto w Tab. 25, która ma kluczowe znaczenie dla formułowania wniosków ekostratygraficznych.

Jednorazowe pojawienie się w basenie na krótki przeciąg czasu – od kilkuset do miliona kilkuset tysięcy lat – taksonów występujących wyłącznie w danej zonie przemawia w większości przypadków za migracyjnym charakterem tych zespołów. Wskazuje na to także wysoka specjalizacja niektórych taksonów (np. *Argyropelecus*), która musiała dokonać się poza basenem karpackim – w Indo-Pacyfiku (por. Jerzmańska & Kotlarczyk 1981). Zanik pewnych taksonów mógł być też związany z wymieraniem (np. *Eovinciguerrria talgiensis* (Dan.) zóna 1, *Eophycis jammensis* Jerz. – zóna 2) lub radykalną zmianą warunków środowiska (np. *Scopeloides* sp. – zóna 1).

8. Analiza następstwa zespołów ichtiofauny umożliwiła skorygowanie poprzednio przeprowadzonej zonacji i sformalizowanie na nowo wszystkich wyróżnionych zón i subzón ekostratygraficznych (Fig. 20). Zdefiniowano zony IPM4A i IPM7 oraz przeprowadzono redefinicję pozostałych zón. Trzy zony mają charakter zón zasięgu taksonu (IPM4, IPM5, IPM6), trzy dalsze – zón zespołowych (IPM1, IPM4A, INM1), dwie kolejne – zón współwystępowania (IPM2, IPM3), a jedna (IPM7) – zony niesamoistnej lub tzw. zony kolejnych ostatnich pojawień.

Zdefiniowano dwie subzony: IPM2 – T.SUB. i INM – L.SUB., oraz zredefiniowano subzonę IPM1 – C.SUB. Z uwagi na brak danych co do czasowego zasięgu epiboli *Syngnathus incompletus* nie redefiniowano subzony IPM6 – S.SUB. Dla wszystkich wyróżnionych zón i subzón określono ich stratotypy i stratotypy granic.

Zebrany materiał pozwolił na wyróżnienie masowych pojawień się taksonu *Centriscus* jako: pierwsze zdarzenie centriskusowe w dolnym rupelu (ok. 32,5 mln lat) i drugie zdarzenie centriskusowe w górnym rupelu (ok. 29,3 mln lat) (Fig. 20).

Celem zbadania zmienności lateralnej zespołów ichtiofauny w obrębie zaproponowanych 9 ichtiozon utworzono podzespoły, złożone z ryb zebranych w odkrywkach podstawowych i uzupełniających (Tab. 26), oddzielnie dla każdej z wyróżnionych 8 stref powierzchniowych (por. Fig. 9).

Okazało się, że powszechne rozprzestrzenienie mają w badanym obszarze zespoły zon: IPM1, IPM2 i IPM4 (Tab. 27, Tab. 28, Tab. 30). W jednostce śląskiej nie stwierdzono zespołów zon: IPM3, IPM5, IPM6 i IPM7 (Tab. 29, Tab. 31–33), jedynie pojedyncze egzemplarze taksonów reprezentujących górny zespół batypelagiczny (Łodygowice, Tab. 19). Jest to rezultat niezastnienia w tej jednostce odpowiednich warunków pogrzebania i zakonserwowania trupów rybich. Nieobecność w jednostce śląskiej i podśląskiej ryb zony INM1 (Tab. 34) wynika przede wszystkim z braku osadów odpowiedniego wieku. Ograniczenie występowania zespołu zony IPM4A (Tab. 30) do jednostki podśląskiej i śladowo do jednostki borysławsko-pokuckiej związane jest ze specyficznymi warunkami ekologicznymi panującymi na skłonach basenu. Nieco mniejszy zasięg rozprzestrzenienia zon IPM3. i IPM5. w porównaniu do zon: IPM4., IPM6. i IPM7. w obszarze jednostki skolskiej zapewne wynika z wykształcenia facjalnego osadów tych zon, niesprzyjającego zachowaniu ichtiotanatoceoz – utlenione osady piaskowców i łupków, a po części z mniej intensywnych poszukiwań zespołów tych zon.

9. Przeprowadzona analiza paleoekologiczna, przy wykorzystaniu informacji o środowiskach bytowania żyjących do dziś taksonów, bądź form najbliższych taksonom wymarłym, pozwoliła wyróżnić w materiale kopalnym kilka grup ekologicznych ichtiofauny: epipelagiczną (EP), mezopelagiczną (MP), batypelagiczną (BP), bentopelagiczną (BEP), demersalną i batydemersalną (D + BD), nerytyczną (N) i związaną ze środowiskiem rafowym (R).

W tym aspekcie zostały scharakteryzowane zespoły 9 wyróżnionych zon (Fig. 21–29). Okazało się, że: 1. we wszystkich tych zespołach duży udział mają ryby EP i BEP; 2. ryby z grup MP i BP występują licznie jedynie w zonach IPM1, IPM3, IPM4, IPM6 i IPM7; 3. ryby D+BD stanowią istotny procent jedynie w zonach IPM2 i IPM4A; 4. ryby z grupy N+R w znaczącej ilości występują jedynie w zonie IPM5.

Uwzględniając udziały wszystkich grup ekologicznych w zespołach zonalnych można zaobserwować wystąpienie 3 wzorów składu zon (Fig. 30, 31). Pierwszy wzór pojawia się w zonach, w których zdecydowaną przewagę mają ryby EP+MP+BP nad rybami BEP+D+BD+N+R (są to zony wym. wyżej w pkt. 2). Wzór drugi charakteryzuje się odwrotnym stosunkiem udziału tych grup (występuje on w zonach IPM2, IPM4A i IPM5). Wzór trzeci pojawia się tylko w zonie INM1, gdzie bez mała wyłącznie mamy ryby EP i BEP z 2,5-krotną przewagą pierwszych.

10. Powstanie tak różnych zespołów ichtiofauny wynika przede wszystkim z oddziaływania rozmaitych czynników na ich środowisko ekologiczne, tempa ewolucji ryb i migracji nowych taksonów, a także jest rezultatem konfiguracji dna basenu.

Zespoły wzoru pierwszego tworzyły się od początku do końca oligocenu. Skład ichtiofauny wskazuje na dość głęboki basen – sięgający poniżej 2000 m. Powszechne rozprzestrzenienie ryb EP-MP-BP w tanacenozach jest w pełni zrozumiałe; stanowią one element autochtoniczny. Równie szerokie rozprzestrzenienie ryb BEP, żyjących tylko do głębokości 400–500 m (niekiedy 1000 m) i ryb D+BD, bytujących do głębokości 200 m (niekiedy do 500 m), a także ryb ze środowiska nerytycznego i rafowego dowodzi intensywnie i szybko działającego transportu pośmiertnego. Wszystkie te ryby stanowią element allochtoniczny tanatocenozy.

Powstanie pod koniec sedymentacji osadów w basenie skolskim zespołu wzoru trzeciego, pozbawionego form MP i BP, a obfitującego w taksony tolerujące środowisko brakiczne, można wyjaśnić znacznym spłyceniem zbiornika w wyniku jego zasypania przez liczącą ok. 1 km pryzmę osadów.

Wyjaśnienie przyczyn powstania zespołów wzoru drugiego, wymaga odrębnego omówienia każdego z 3 przypadków. Obecność w zespole IPM4A wszystkich grup ekologicznych, i to w znaczącej ilości, można dobrze wyjaśnić tworzeniem się tanatocenozy na skłonie grzbietu podmorskiego, gdzie żyły ryby thalassobentopelagialu i dokąd mogły łatwo być znoszone ryby z thalasso-epibentalu i thalasso-epipelagialu.

Największą trudność stwarza wyjaśnienie powstania zony IPM2. Poprzednia wersja tłumacząca eliminację ryb MP i BP ze zbiornika obniżeniem lustra wody w wysychającym basenie (*desiccation basin*), wydaje się obecnie mniej prawdopodobna od opcji, w myśl której w N basenie Tetydy (Paratetyda) zaistniały okresowo warunki anaerobowe. Utrzymujące się w osadzie, bez mała przez cały czas sedymentacji formacji menilitowej, warunki beztlenowe spowodowane wysoką zawartością TOC, w omawianym okresie objęły także dolną część toni wody po izobacie 500 m. Sytuacja ta umożliwiła przeżycie taksonom żyjącym na szelfie, a także związanym z krawędzią szelfu i górna częścią skłonu, natomiast wymusiła eliminację ryb głębokomorskich. Mechanizm roznoszenia taksonów płytkowodnych na całe dno basenu był zapewne podobny jak w przypadku opisywanych wyżej zespołów wzoru pierwszego. Na allochtoniczny charakter powstałych w IPM2 tanatocenozy zdaje się wskazywać także mniejsza ilość kopalnych ryb wydobytych z 1m profilu tej zony, w porównaniu z ilością ryb wydobytych z podobnego odcinka profili zon batypelagicznych, a z drugiej strony wystąpienie w środku basenu warstewki przepelnionej osobnikami gatunków płytkowodnych (zdarzenie trachinusowe). Zaistnienie w toni basenu strefy minimum tlenowego można wiązać z gwałtownym zmniejszeniem dopływu wód utlenionych z oceanu przez rów Renu i korytarz słoweński (Rögl, 1999), na co z kolei mogło wpłynąć obniżenie poziomu morza o ok. 25–30 m datowane na ok. 31,5 mln lat BP.

Największe w paleogenie, ok. 28,5 mln lat BP, obniżenie poziomu morza szacowane na 175 m (Fig. 33) jest odpowiedzialne natomiast za uformowanie się zony zespołu IPM5. Zepchnięte wówczas w pobliże krawędzi szelfu zespoły ryb N i R (także D), mogły łatwo zasilać tanatocenozy, tworzące się na skłonie i podniesieniu kontynentalnym. Dzięki temu zespoły autochtoniczne obfitujące w bentopelagiczne taksony głębokowodne (Alepocephalidae) zostały uzupełnione o obfitą komponentę, typową dla środowisk płytkowodnych (Tab. 32). Obserwowanemu wzbogaceniu tanatocenozy w taksony bentopelagiczne (m.in. *Lepidopus*, *Carpathichthys*, *Zeus*) towarzyszy gwałtowny spadek udziału ryb mezo- i batypelagicznych (*Eomyctophum*, *Idrissia*, *Vinciguerria*) (Fig. 30, 32). Mógł on być spowodowany utworzeniem się strefy minimum tlenowego w górnej części mezobatialu. Z drugiej strony obecność bardzo głębokowodnych Alepocephalidae wskazuje na dobre połączenie karpackiego basenu Tetydy z otwartym oceanem (typu głębokiej cieśniny Gibraltaru), które nie zostało przerwane podczas największego w paleogenie obniżenia poziomu morza.

Syntezę powiązania zaproponowanej zonacji ichtiofaunistycznej z lito-, bio- i chronostratygrafią serii menilitowo-krośnieńskiej, a także z przebiegiem krzywej eustatycznej (dostosowanej do geochronologii i chronostratygrafii Berggren *et al.*, 1995) przedstawiono na Fig. 33.

Figures

3, 4, 6

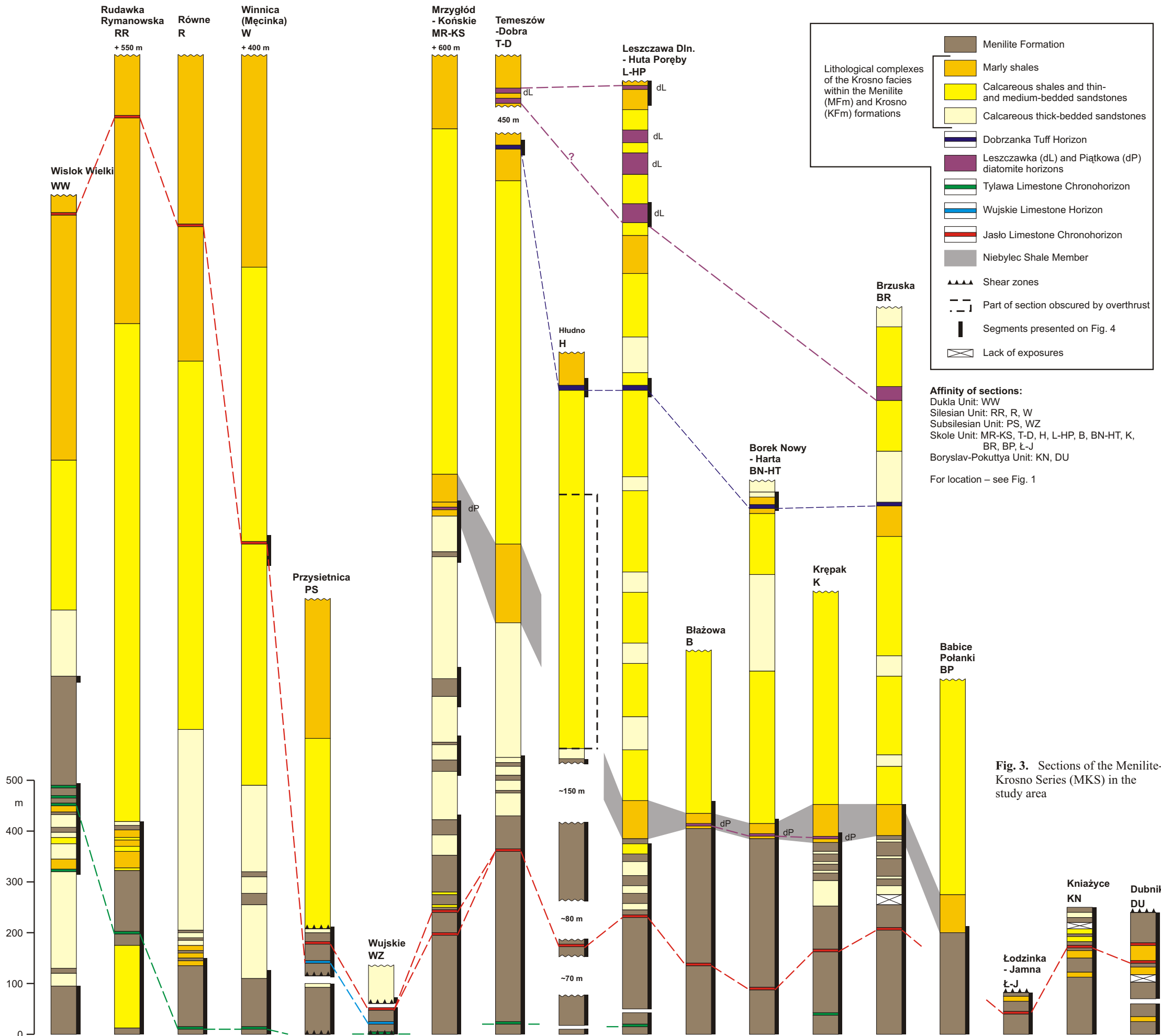


Fig. 3. Sections of the Menilite-Krosno Series (MKS) in the study area

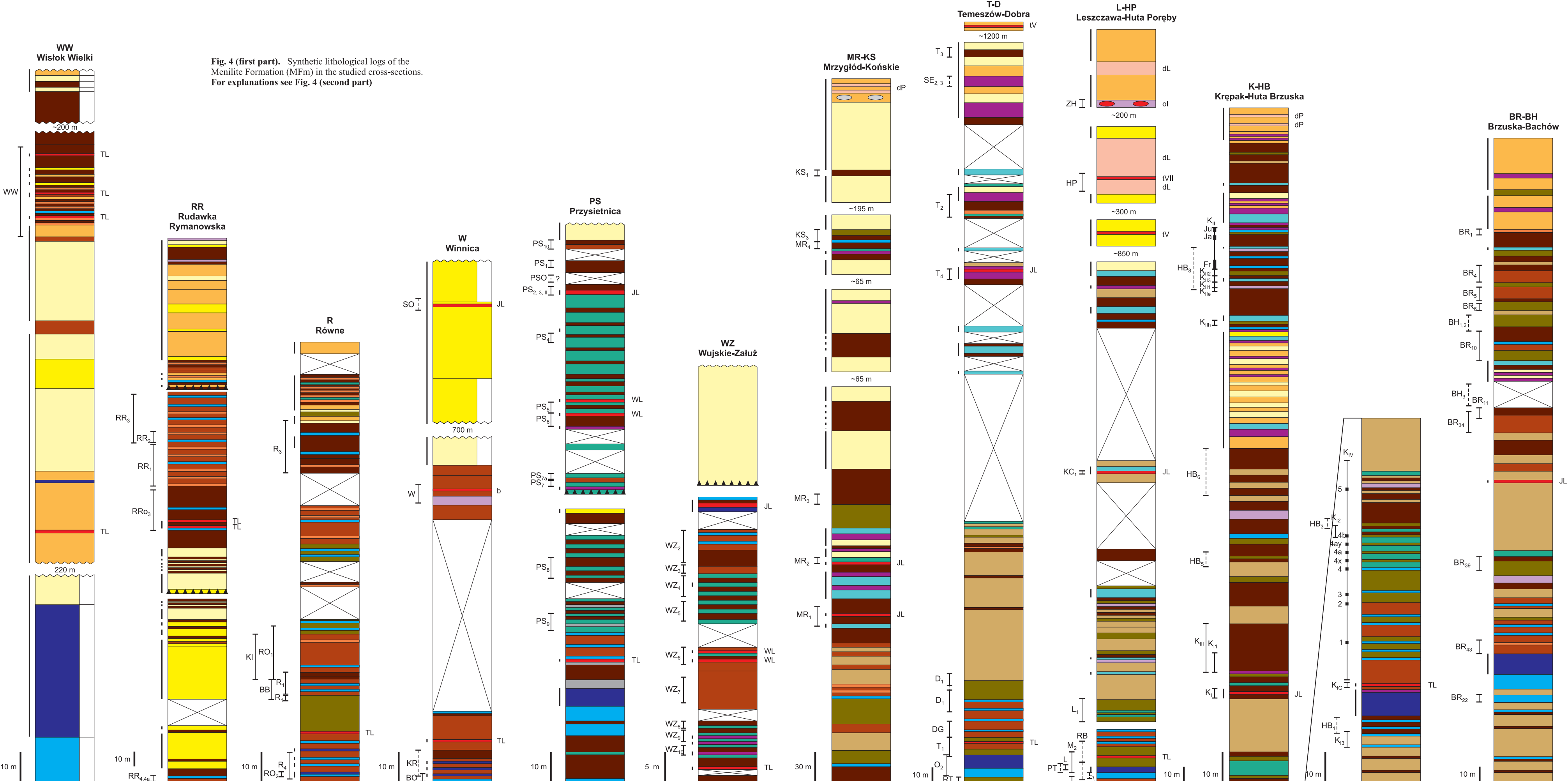


Fig. 4 (first part). Synthetic lithological logs of the Menilite Formation (MFm) in the studied cross-sections. For explanations see Fig. 4 (second part)

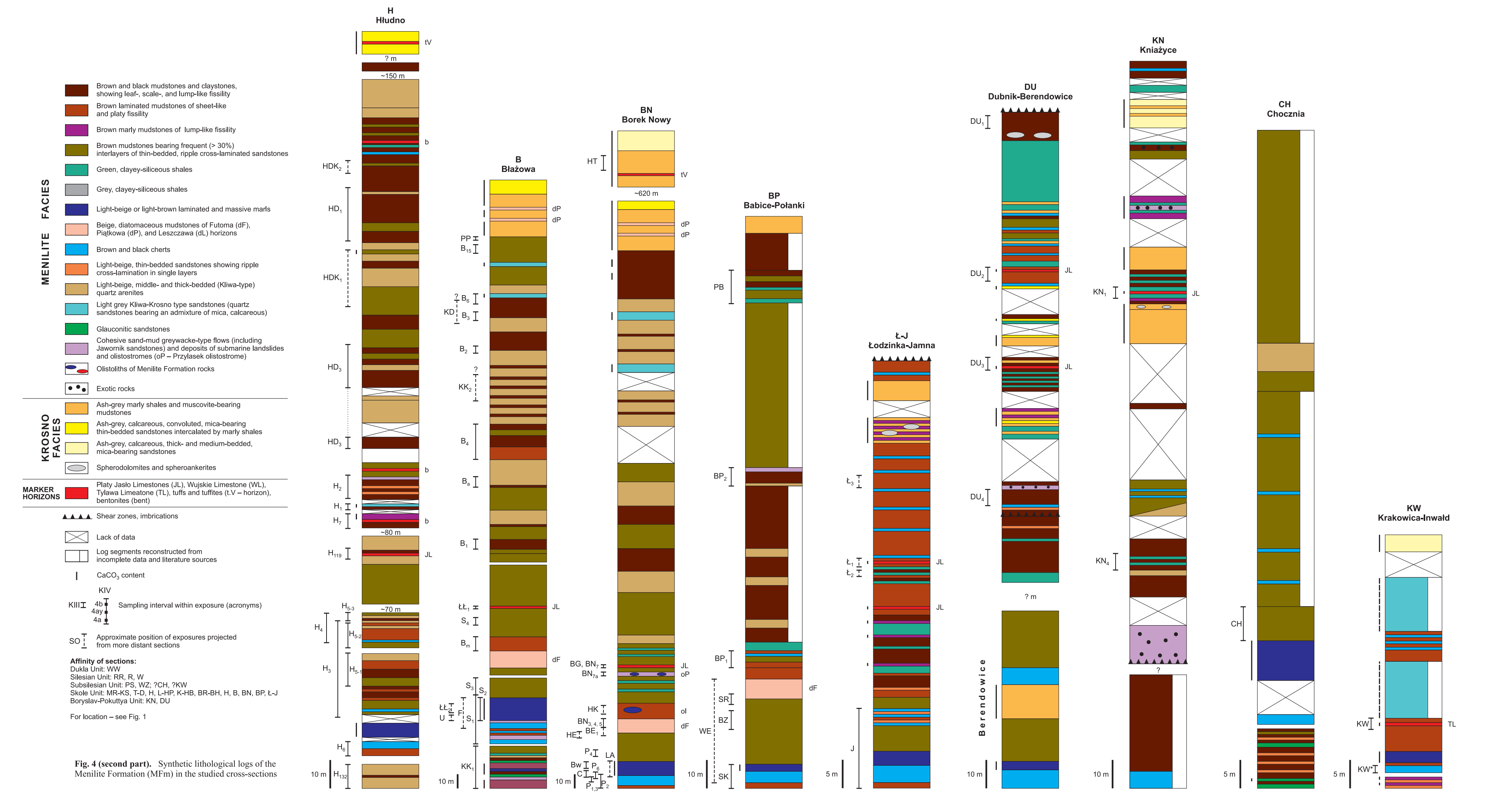
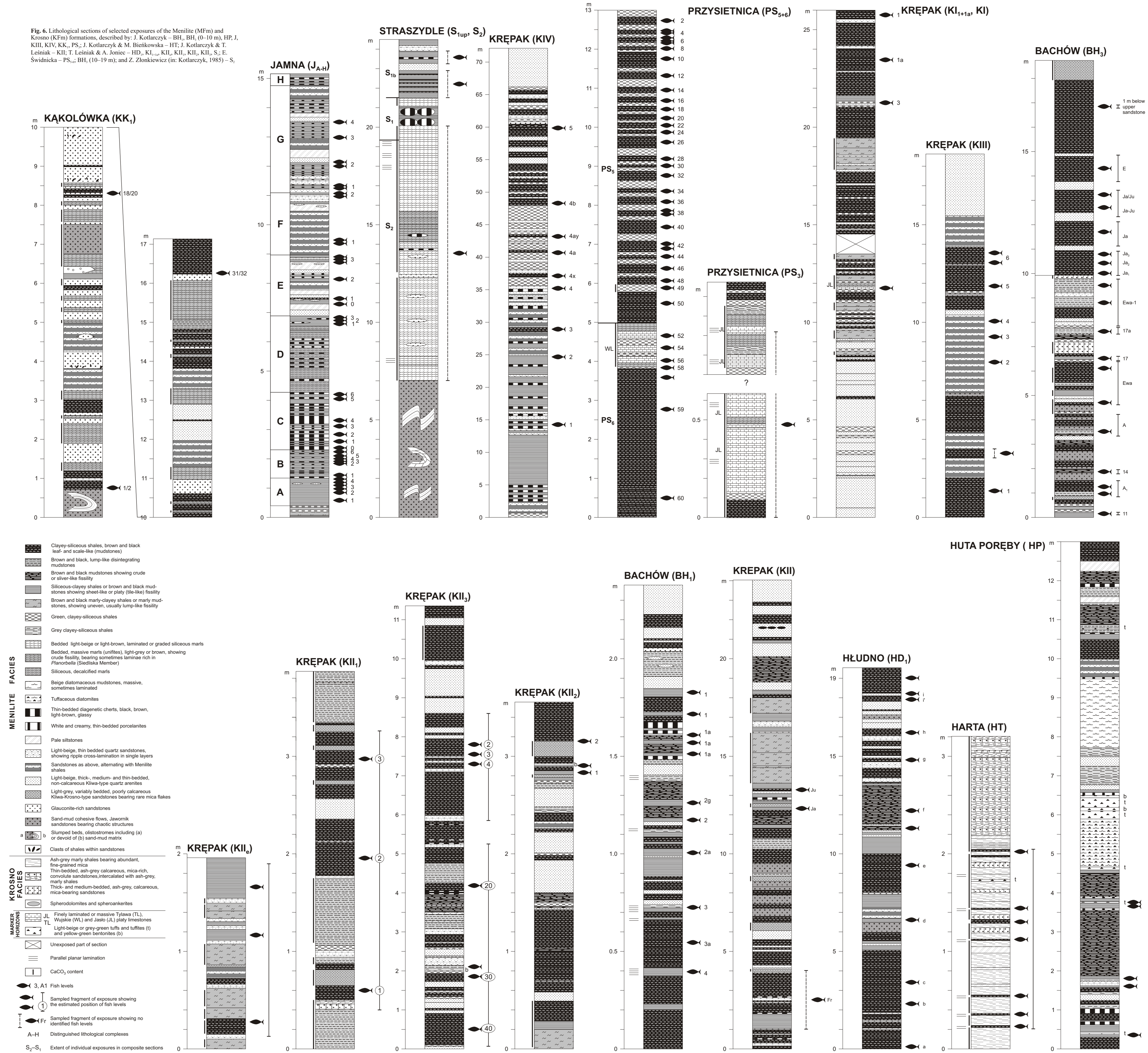


Fig. 4 (second part). Synthetic lithological logs of the Menilite Formation (MFm) in the studied cross-sections

Fig. 6. Lithological sections of selected exposures of the Menilite (Mfm) and Krosno (Kfm) formations, described by: J. Kotlarczyk & M. Bienkowska - BH₁, BH₂ (0-10 m), HP, J, KIII, KIV, KK₁, PS₃; J. Kotlarczyk & T. Leśniak - HT; J. Kotlarczyk & T. Leśniak - KII; T. Leśniak & A. Joniec - HD, KI₁₊₂, KII₁, KII₂, KII₃, S₁; E. Świdnicka - PS₅; BH₃ (10-19 m); and Z. Zlonkiewicz (in: Kotlarczyk, 1985) - S₂.



Tables

4–23, 25, 27–34

Table 5

Variability of ichthyofaunal assemblages among stratigraphically arranged fish levels at exposure Křepak IV

Level	<i>Clupea</i> sp.	<i>Glossanodon</i> sp.	<i>Palaeogadus</i> sp.	<i>Serranus</i> sp.	<i>Bregmaceros filamentosus</i>	<i>Lepidopus</i> sp.	<i>Polyipnus brevis</i>	<i>Vinciguerria</i> sp.	<i>Kollarzykia bathybia</i>	<i>Zenopsis</i> sp.	<i>Bathyrion</i> sp.	<i>Idrissia</i> sp.	<i>Palaeorhynchus</i> sp.	<i>Clupea sardinites</i>	<i>Eomycophum</i> sp.	<i>Hemithyrsites</i> sp.	<i>Polyipnus cf. anteasteroides</i>	<i>Scorpaenoides</i> sp.	<i>Solenorhynchus</i> sp.	<i>Thyrstoides</i> sp.	<i>Vinciguerria distincta</i>	<i>Hemithyrsites rumanus</i>	Antennariidae	Fistulariidae	Scombridae	Gempylidae	Gonostomatidae	Apogonidae	Sternoptychidae	Beryciformes	Gadiformes	Perciformes (typus-à la, à la')	Salmoniformes ? (typus-xx')	Scomroidei	Number of individuals		
KIV																																					20
5																																					52
4b																																					4
4 _{Ay}																																					11
4a																																					26
4x																																					5
4																																					30
3																																					4
2																																					4
1																																					4

The KIV level assemblage is derived from unidentified layers situated close to layer 5

$\Sigma = 160$



Assemblages derived from those levels which are marked by letters devoid of numbers were collected from the entire lithological complex labelled by this letter, without taking into account individual layers. Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800

Table 7

Variability of ichthyofaunal assemblages among stratigraphically arranged fish levels at exposures Krępak I, I_{1+1a}, and III (KI, KI_{1+1a}, KIII)

Exposure	Level	<i>Palaeorhynchus</i> sp.	<i>Polyipnus</i> cf. <i>sobnioviensis</i>	<i>Zeus faber</i>	<i>Africentrum</i> sp.	<i>Alosa</i> sp.	<i>Lepidopus</i> sp.	<i>Priacanthus</i> sp.	<i>Vinciguerra</i> sp.	<i>Clupea</i> sp.	<i>Eomyctophum</i> sp.	<i>Merluccius</i> sp.	<i>Holocentroides</i> sp.	<i>Idrissia</i> sp.	<i>Scorpaenoides</i> sp.	<i>Serranus</i> sp.	<i>Hemithyrsites</i> sp.	<i>Pinichthys</i> sp.	<i>Scomber voitestii</i>	<i>Carpathichthys polonicus</i>	<i>Apostasis</i> sp.	<i>Sarda</i> sp.	Gonostomatidae	Sternoptychidae	Gempylidae	Myctophidae	Scombridae	Bathylagidae (typus-"Melania")	Beryciformes	Pleuronectiformes	Perciformes (typus-"à la, à la")	Anguilliformes	Perciformes	Scombroidei	Genus indet.	Number of individuals			
KIII	6	1																																				6	
	4																																						6
	3									1																												27	
	2																																					11	
	1									1																												23	
KI ₁	1																																					8	
	1a									1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	19	
	3																																					12	
KI	KI																																				3		



Σ = 115

Assemblages derived from those levels which are marked by letters devoid of numbers were collected from the entire lithological complex labelled by this letter, without taking into account individual layers. Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800

Table 13

Variability of ichthyofaunal assemblages among stratigraphically arranged exposures in the composite section of Zone V:
Leszczawa - Hłudno.

Taxon	Exposure	KT _{B,C,D} KC _{2'} M ₁ , PT, M _{2bp}	H ₁₃₂ H ₆	L	M _{2up}	RB _{1,2,3}	H ₃₃ H ₄₄ H ₅₅ H _{DS}	L ₁	KC ₁ H ₁₁₉	H ₇₇ H ₁₁ , H ₂₂	HD ₃	HD ₁₁ , HD ₂₂	HDK ₁	ŁH _{1,2}	HP	ZH
<i>Centriscus longispinus</i>																
<i>Centriscus</i> sp.																
<i>Cetorhinus</i> sp.																
<i>Clupea sardinites</i>																
<i>Eomyctophum limicola</i>																
<i>Lepidopus glarianus</i>																
<i>Vinciguerria obscura</i>																
<i>Palimphyes</i> sp.																
<i>Vinciguerria</i> sp.																
<i>Lepidopus</i> sp.																
<i>Clupea</i> sp.																
<i>Eomyctophum</i> sp.																
<i>Centriscus heinrichi</i>																
<i>Scopeloides</i> sp.																
<i>Vinciguerria talgiensis</i>																
<i>Capros radobojanus</i>																
<i>Eophycis jamnensis</i>																
<i>Eophycis</i> sp.																
<i>Glossanodon musceli</i>																
<i>Glossanodon</i> sp.																
<i>Palaeogadus simionescui</i>																
<i>Palaeogadus</i> sp.																
<i>Serranus budensis</i>																
<i>Serranus</i> sp.																
<i>Trachinus minutus</i>																
<i>Holosteus</i> sp.																
<i>Properca</i> sp.																
<i>Sarda</i> sp.																
<i>Ammodytes antipai</i>																
<i>Fistularia</i> sp.																
<i>Hemiramphus jerzyi</i>																
<i>Pomolobus</i> sp.																
<i>Caranx</i> sp.																
<i>Alosa</i> sp.																
<i>Kotlarczykia bathybia</i>																
<i>Lepidopus isopleurus</i>																
<i>Mugil</i> sp.																
<i>Palaeorhynchus</i> sp.																
<i>Polyipnus brevis</i>																
<i>Zenopsis clarus</i>																
<i>Polyipnus sobniowiensis</i>																
<i>Eomyctophum</i> cf. <i>koraense</i>																
<i>Vinciguerria merklinii</i>																
<i>Idrissia</i> sp.																
<i>Argyropelecus</i> sp.																
<i>Merluccius</i> sp.																
<i>Priacanthus</i> sp.																
<i>Syngnathus</i> sp.																
<i>Vinciguerria distincta</i>																
<i>Holocentroides moldavicus</i>																
<i>Africentrum</i> sp.																
<i>Echeneis carpathica</i>																
<i>Hemithyrsites</i> sp.																
<i>Glyptophidium</i> sp.																
<i>Notidanus</i> sp.																
<i>Palaeogadus distinctus</i> n.sp.																
<i>Palaeogadus intergerinus</i>																
<i>Parasteindachneria oligocaenica</i> n. sp.																
<i>Scorpaenoides</i> sp.																
<i>Thyrstitoides</i> sp.																
<i>Syngnathus</i> sp. (typus A)																
<i>Merluccius errans</i>																
<i>Caranx gracilis</i>																
Gadidae																
Gonostomatidae																
Myctophidae (typus-"Giant-II")																
Apogonidae																
Clupeidae																
Gempylidae																
Scombridae																
Bathylagidae (typus-"Melania")																
Sternoptychidae (typus-"xz")																
Bathylagidae																
Aulorhynchidae																
Gadiformes																
Anguilliformes																
Beryciformes																
Perciformes																
Pleuronectiformes																
Stomiiformes																
Perciformes (typus-"à la, à la")																
Salmoniformes ? (typus-"xx")																
Percoidei																
Genus indet.																

Indices bp or up which accompany exposure acronyms mark either the lower or upper part of bed sequence of this exposure



Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 14

Variability of ichthyofaunal assemblages among stratigraphically arranged exposures in the composite section of Zone VI: Temeszów - Mrzyglód

Taxon	Exposure	O ₂	T ₁	DG	D ₁	MR ₁ +T ₄	T ₂ MR ₂ MR ₃	T ₃ SE ₁₋₃	MR ₄ KS ₃	KS ₁
<i>Cetorhinus</i> sp.		█								
<i>Clupea</i> sp.					█			█		
<i>Eomyctophum</i> sp.		█				---		█	█	
<i>Lepidopus</i> sp.		█					---	█		
<i>Palaeorhynchus</i> sp.		---						█		
<i>Scopeloides</i> sp.		█								
<i>Serranus</i> sp.		---	█	█	█					
<i>Vinciguerria</i> sp.		█								
<i>Glossanodon</i> sp.			█		█					
<i>Palaeogadus</i> sp.				█	█					
<i>Properca</i> sp.			█							
<i>Clupea sardinites</i>				█	█	---		█		
<i>Palaeogadus simionescui</i>				█	█					
<i>Pinichthys</i> sp.				█	█					
<i>Sarda</i> sp.				---						
<i>Serranus budensis</i>				█	█					
<i>Caranx petrodavae</i>					---					
<i>Glossanodon musceli</i>					█					
<i>Eomyctophum</i> cf. <i>koraense</i>						█				
<i>Merluccius</i> sp.							---		█	
<i>Polyipnus sobnioviensis</i>						█				
<i>Polyipnus</i> cf. <i>sobnioviensis</i>						█				
<i>Idrissia</i> sp.						█		█		
<i>Syngnathus</i> sp.							---			
<i>Alosa</i> sp.								█		
<i>Holocentroides moldavicus</i>								█		
<i>Africentrum</i> sp.								█		
<i>Carpathichthys polonicus</i>								█		
<i>Argyrolepecus</i> sp.									---	
<i>Syngnathus incompletus</i>										---
Argentinidae		█								
Clupeidae		---						█		
Gonostomatidae		█								
Myctophidae		█						---		
Sternoptychidae		█								
Gadidae			█							
Gempylidae								█	---	
Sternoptychidae (typus "xz")								█		
Bathylagidae (typus "Melania")								---		
Gadiformes		---	█							
Pleuronectiformes		█								
Perciformes (typus "à la, à la")				---				█		
Perciformes					█				---	
Salmoniformes ?(typus "-xx")								---		
Stomiiformes								---		
Percoidei			---							
Genus indet.		█		█						

 0 1 2 3 4 5 6 7 8 9
 Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 15

Variability of ichthyofaunal assemblages among stratigraphically arranged exposures in the composite section of Zone II: Babice - Wola Węgierska. For other explanations see Table 13

Taxon	Exposure	WE _{bp}	SK	WE _{up}	BZ BP ₁	SR	BP ₂	PB
<i>Alosa</i> sp.		-----						
<i>Centriscus longispinus</i>		-----						
<i>Centriscus</i> sp.		-----	-----					
<i>Clupea</i> sp.		-----	-----	-----	-----		-----	-----
<i>Eomyctophum</i> sp.		-----	-----				-----	-----
<i>Glossanodon</i> sp.		-----	-----	-----	-----			
<i>Lepidopus</i> sp.		-----	-----	-----			-----	-----
<i>Palaeorhynchus</i> sp.		-----	-----					
<i>Palimphyes</i> sp.		-----	-----					
<i>Polyipnus</i> sp.		-----	-----					
<i>Scopeloides</i> sp.		-----	-----					
<i>Vinciguerria</i> sp.		-----	-----				-----	
<i>Centriscus heinrichi</i> ♀			-----					
<i>Centriscus heinrichi</i> ♂			-----					
<i>Centriscus teleajensis</i>			-----					
<i>Clupea sardinites</i>			-----				-----	
<i>Diaphus</i> sp.			-----					
<i>Eomyctophum limicola</i>			-----					
<i>Scopeloides glarisianus</i>			-----					
<i>Scorpaenoides popovicii</i>			-----					
<i>Scorpaenoides</i> sp.			-----					
<i>Syngnathus</i> sp.			-----					-----
<i>Vinciguerria distincta</i>			-----					
<i>Vinciguerria obscura</i>			-----					
<i>Capros</i> sp.				-----				
<i>Eophycis</i> sp.				-----				
<i>Palaeogadus</i> sp.				-----				
<i>Palaeomolva</i> sp.				-----				
<i>Serranus</i> sp.				-----				
<i>Trachinus</i> ? sp.				-----				
<i>Palaeogadus simionescui</i>					-----			
<i>Serranus budensis</i>					-----			
<i>Holocentroides moldavicus</i>							-----	
<i>Argyropelecus cosmovicii</i>							-----	
<i>Argyropelecus</i> sp.							-----	
<i>Capros radobojanus</i>							-----	
<i>Eomyctophum cf. koraense</i>							-----	
<i>Eomyctophum menneri</i>							-----	
<i>Glyptophidium</i> sp.							-----	
<i>Hemithyrsites</i> sp.							-----	-----
<i>Idrissia</i> sp.							-----	
<i>Lepidopus glarisianus</i>							-----	
<i>Lepidopus isopleurus</i>							-----	
<i>Merluccius</i> sp.							-----	
<i>Palaeogadus distinctus</i> n.sp.							-----	
<i>Palaeogadus intergerinus</i>							-----	
<i>Parasteindachneria oligocaenica</i> n.sp.							-----	
<i>Properca sabbai</i>							-----	
<i>Scomber voitestii</i>							-----	
<i>Serranus budensis</i>							-----	
<i>Syngnathus</i> sp. (typus A)							-----	
<i>Syngnathus incompletus</i>							-----	
<i>Thyrstitoides</i> sp.							-----	-----
Clupeidae		-----						
Gonostomatidae		-----	-----					
Myctophidae		-----						
Sternoptychidae		-----						
Bathylagidae			-----					
Gadidae			-----					
Scombridae			-----					-----
Myctophidae (typus "Giant-II")			-----					
Gempylidae			-----				-----	
Trichiuridae						-----		
Bathylagidae (typus "Melania")							-----	
Tetraodontiformes		-----						
Clupeiformes			-----					
Salmoniformes ? (typus "xx")			-----					
Gadiformes				-----				
Perciformes						-----		
Anguilliformes							-----	
Beryciformes							-----	
Pleuronectiformes							-----	
Syngnathiformes							-----	
Genus indet.		-----	-----	-----			-----	-----

----- 0 1 2 3 4 5 6 7 8 9

Ranks of taxa frequency refer to the following numbers of specimens:

0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 16

Variability of ichthyofaunal assemblages among stratigraphically arranged exposures in the composite section of Zone I: Jamna Dolna - Łodzinka - Książce - Dubnik

Taxon	Exposure	J _{A-C}	J _{D-G}	DU ₄	KN ₄	Ł ₂	KN ₁	DU ₃	Ł _{1,1A}	DU ₂	Ł ₃	DU ₁
<i>Ammodytes antipai</i>		-----										
<i>Capros radobojanus</i>		-----										
<i>Caranx petrodavae</i>		-----										
<i>Centriscus heinrichi</i> ♀		-----										
<i>Centriscus heinrichi</i> ♂		-----										
<i>Centriscus longispinus</i>		-----										
<i>Centriscus</i> sp.		-----										
<i>Centriscus teleajensis</i>		-----										
<i>Clupea sardinites</i>		-----										
<i>Clupea</i> sp.		-----										
<i>Eomyctophum limicola</i>		-----										
<i>Lepidopus glarianus</i>		-----										
<i>Lepidopus</i> sp.		-----										
<i>Palaeorhynchus</i> sp.		-----										
<i>Palimphyes lanceolata</i>		-----										
<i>Palimphyes</i> sp.		-----										
<i>Scomber voitestii</i>		-----										
<i>Scopeloides glarianus</i>		-----										
<i>Scopeloides</i> sp.		-----										
<i>Thyrsitoides</i> sp.		-----										
<i>Vinciguerria distincta</i>		-----										
<i>Vinciguerria obscura</i>		-----										
<i>Vinciguerria</i> sp.		-----										
<i>Zenopsis clarus</i>		-----										
<i>Zenopsis</i> sp.		-----										
<i>Cetorhinus</i> sp.		-----										
<i>Eophycis jamnensis</i>			-----									
<i>Eophycis</i> sp.			-----									
<i>Glossanodon musceli</i>			-----									
<i>Glossanodon</i> sp.			-----									
<i>Hipposyngnathus neriticus</i>			-----									
<i>Holosteus</i> sp.			-----									
<i>Palaeogadus abbreviatus</i>			-----									
<i>Palaeogadus simionescui</i>			-----									
<i>Propercarina</i> sp.			-----									
<i>Serranus budensis</i>			-----									
<i>Serranus</i> sp.			-----									
<i>Syngnathus incompletus</i>						-----						
<i>Syngnathus</i> sp.						-----						
<i>Trachinus minutus</i>			-----									
<i>Trachinus</i> sp.			-----									
<i>Eomyctophum cf. koraense</i>				-----								
<i>Eomyctophum</i> sp.				-----								
<i>Forcipiger</i> sp.					-----							
<i>Holocentroides</i> sp.						-----						
<i>Oligolactoria bubiki</i>						-----						
<i>Idrissia</i> sp.							-----					
<i>Holocentroides moldavicus</i>								-----				
<i>Eomyctophum menneri</i>								-----				
<i>Alosa</i> sp.									-----			
Bathylagidae		-----										
Gonostomatidae		-----										
Myctophidae (typus-"Giant-II")		-----										
Scombridae		-----										
Scorpaenidae		-----										
Sternoptychidae (typus "xz")		-----										
Clupeidae						-----						
Gempylidae									-----			
Beryciformes		-----										
Pleuronectiformes		-----										
Perciformes									-----			
Scombroidei										-----		
Genus indet.		-----										



Ranks of taxa frequency refer to the following numbers of specimens:

0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 17

Variability of ichthyofaunal assemblages among stratigraphically arranged exposures in the Przysietnica synthetic section, Zone VII

Taxon	Exposure	PS ₇	PS ₆₊₅	PS ₃₊₂	PS ₀	PS ₁	PS ₁₀	PS ₈
<i>Apostasis</i> sp.								
<i>Bregmaceros filamentosus</i>								
<i>Bregmaceros</i> sp.								
<i>Clupea</i> sp.								
<i>Echeneis carpathica</i>								
<i>Eomyctophum</i> sp.								
<i>Idrissia</i> sp.								
<i>Kotlarczykia bathybia</i>								
<i>Kotlarczykia</i> sp.								
<i>Lepidopus</i> sp.								
<i>Palaeogadus</i> sp.								
<i>Palaeomolva</i> sp.								
<i>Palaeorhynchus</i> sp.								
<i>Polyipnus brevis</i>								
<i>Polyipnus</i> sp.								
<i>Priacanthus</i> sp.								
<i>Properca</i> sp.								
<i>Propercarina</i> sp.								
<i>Scorpaenoides</i> sp.								
<i>Serranus</i> sp.								
<i>Syngnathus</i> sp.								
<i>Zenopsis</i> sp.								
<i>Zeus</i> sp.								
<i>Africentrum</i> sp.								
<i>Alosa</i> sp.								
<i>Antigonia</i> sp.								
<i>Capros radobojanus</i>								
<i>Capros</i> sp.								
<i>Caprovesposus</i> sp.								
<i>Carpathospinosus propheticus</i>								
<i>Carpathospinosus</i> sp.								
<i>Centriscus nov. sp.</i>								
<i>Centriscus</i> sp.								
<i>Eomyctophum cf. koraense</i>								
<i>Fistularia</i> sp.								
<i>Forcipiger</i> sp.								
<i>Hemithyrsites</i> sp.								
<i>Holocentroides</i> sp.								
<i>Holosteus</i> sp.								
<i>Oligobalistes</i> sp.								
<i>Onobrosmius</i> sp.								
<i>Parahollandia ? sp.</i>								
<i>Psenicubiceps</i> sp.								
<i>Scomber voitestii</i>								
<i>Scorpaena</i> sp.								
<i>Syngnathus</i> sp. (typus A)								
<i>Thyrsitoides</i> sp.								
<i>Zeus faber</i>								
<i>Eomyctophum menneri</i>								
<i>Polyipnus cf. anteasteroides</i>								
<i>Polyipnus cf. sobnioviensis</i>								
<i>Argyropelecus</i> sp.								
<i>Glyptophidium</i> sp.								
<i>Merluccius</i> sp.								
<i>Palaeogadus distinctus</i> n.sp.								
<i>Parasteindachneria oligocaenica</i> n.sp.								
<i>Syngnathus incompletus</i>								
<i>Vinciguerria</i> sp.								
<i>Syngnathus</i> sp. (typus B)								
<i>Carpathichthys polonicus</i>								
Apogonidae								
Balistidae								
Gempylidae								
Gonostomatidae								
Scombridae								
Sternoptychidae (typus "xz")								
Thunninae								
Antennariidae								
Aulorhynchidae								
Aulostomidae								
Bathylagidae (typus "Melania")								
Caproidae								
Clupeidae								
Myctophidae (typus "Giant-II")								
Nomeidae								
Paralepididae								
Sternoptychidae								
Triacanthodidae								
Trichiuridae								
Zeidae								
Psettodidae								
Alepocephalidae								
Myctophidae								
Anguilliformes								
Beryciformes								
Gadiformes								
Perciformes								
Tetraodontiformes								
Zeiformes								
Perciformes (typus-"à la, à la")								
Pleuronectiformes								
Salmoniformes								
Syngnathiformes								
Stomiiformes								
Percoidei								
Scombroidei								
Stromateoidei								
Genus indet.								
Genus indet.-typus A								
Genus indet.-typus P								
Elasmobranchii								

0 1 2 3 4 5 6 7 8 9

Ranks of taxa frequency refer to the following numbers of specimens:

0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 18

Variability of ichthyofaunal assemblages among stratigraphically arranged exposures in the composite section of Zone VIII: Rudawka Rymanowska, Równe, Wisłok W, Winnica. The second to last column shows a composite fish assemblage of the first four columns; whereas the last column portrays the assemblage of the remaining outcrops, except for SO

Taxon	Exposure	RR ₄	RO ₂	BO	KR _o	RR ₁₋₃	RO ₁	R _{1,4}	KL	BB	WW	KR	W	SO	IPM1	IPM2
		RR _{4a}				RR ₀₃									Σ ₁	Σ ₂
<i>Alosa</i> sp.																
<i>Cetorhinus</i> sp.																
<i>Clupea sardinites</i>																
<i>Clupea</i> sp.																
<i>Lepidopus</i> sp.																
<i>Palimphyes</i> sp.																
<i>Scopeloides</i> sp.																
<i>Ammodytes antipai</i>																
<i>Palaeogadus</i> sp.																
<i>Propercarina</i> sp.																
<i>Scomber voitestii</i>																
<i>Serranus budensis</i>																
<i>Serranus</i> sp.																
<i>Capros radobojanus</i>																
<i>Caranx petrodavae</i>																
<i>Eophycis</i> sp.																
<i>Glossanodon musceli</i>																
<i>Glossanodon</i> sp.																
<i>Hemiramphus jerzyi</i>																
<i>Leiognathus</i> sp.																
<i>Palaeogadus simionescui</i>																
<i>Palaeorhynchus</i> sp.																
<i>Properca sabbai</i>																
<i>Syngnathus incompletus</i>																
<i>Fistularia</i> sp.																
<i>Trachinus ? sp.</i>																
<i>Lepidopus glarisianus</i>																
<i>Eophycis jamnesis</i>																
<i>Holosteus mariae</i>																
<i>Sarda</i> sp.																
<i>Africentrum</i> sp.																
<i>Eomyctophum cf. koraense</i>																
<i>Eomyctophum menneri</i>																
<i>Eomyctophum</i> sp.																
<i>Equula ? sp.</i>																
<i>Hemithysites</i> sp.																
<i>Holosteus</i> sp.																
<i>Idrissia carpathica</i>																
<i>Idrissia</i> sp.																
<i>Merluccius</i> sp.																
<i>Polyipnus cf. anteasteroides</i>																
<i>Polyipnus sobnioviensis</i>																
<i>Polyipnus cf. sobnioviensis</i>																
<i>Polyipnus</i> sp.																
<i>Priacanthus</i> sp.																
Bathylagidae																
Scombridae																
Gadidae																
Myctophidae (typus-"Giant II")																
Gempylidae																
Gadiformes																
Perciformes																
Perciformes (typus-"à la, à la")																
Scorpaenoiformes																
Percoidei																
Scombroidei																
Genus indet.																



Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 19

Variability of ichthyofaunal assemblages among stratigraphically arranged exposures in the composite section of Zone IX: Chocznia - Krakowica - Lodygowice; assemblages known from literature only are marked by asterisks

Taxon \ Exposure	KW*	CH	KW	Wola R.*	ŁW
<i>Centruscus heinrichi</i>	-----				
<i>Lepidopus glarisianus</i>	-----				
<i>Clupea sardinites</i>		-----		-----	-----
<i>Glossanodon musceli</i>		██████	-----		
<i>Lepidopus</i> sp.		=====			-----
<i>Serranus</i> sp.		-----			
<i>Merluccius macroactus</i>				-----	
<i>Alosa</i> sp.					-----
<i>Holocentroides moldavicus</i>					-----
<i>Palaeorhynchus</i> sp.					-----
Sternoptychidae (typus-"xz")					-----

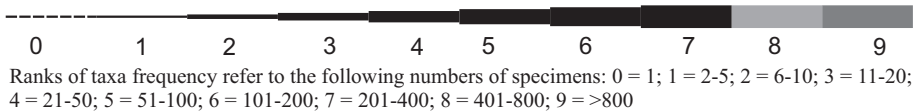


Table 20

Ichthyofaunal assemblages in exposures (or their groups) of the Jaslo Limestone Chronohorizon

Taxon \ Exposure	SO	PS _{2,3} PS _{II}	LL ₁	H ₁₁₉	T ₄	MR ₁	KI	KN ₁	DU ₃	BN ₇	KC ₁	BK ₁
<i>Africentrum</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Clupea</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Clupea sardinites</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Eomyctophum</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Eomyctophum</i> cf. <i>koraense</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Eomyctophum menneri</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Equula?</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Hemithyrsites</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Holocentroides moldavicus</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Holocentroides</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Holosteus</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Idrissia</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Idrissia carpathica</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Lepidopus</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Merluccius</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Oligolactoria bubiki</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Palaeogadus</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Polyipnus</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Polyipnus</i> cf. <i>anteasteroides</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Polyipnus</i> cf. <i>sobnioviensis</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Polyipnus sobnioviensis</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Priacanthus</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Priacanthus longispinus</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Sarda</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Vinciguerria</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Vinciguerria merklini</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Vinciguerria obscura</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Zeus faber</i>	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Alopecias</i> sp.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Number of individuals	342	70	132	13	10	5	2	12	4	1	1	1

Σ = 593

Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 21

Ichthyofaunal assemblages in exposures (or their groups) of the Kotów and Dynów members

Taxon	Exposure	KOTÓW CHERT MEMBER									DYNÓW MARL MEMBER					
		RR ₄	H ₆	KT _{B-D}	P _{1-3,6}	LA	KI ₃	J _{A-C}	SK	WE _{bp}	BO	O ₂	PT	U, F, ŁŁ ₂	S ₁ S ₂	BW HK ₂
<i>Alosa</i> sp.		-----				-----										
<i>Ammodytes antipai</i>								-----								
<i>Barbus</i> sp.													-----			
<i>Capros radobojanus</i>								-----								
<i>Caranx petrodavae</i>								-----								
<i>Centriscus</i> sp.			-----	-----				-----	-----	-----						
<i>Centriscus heinrichi</i>			-----		-----			-----	-----	-----						
<i>Centriscus longispinus</i>				-----				-----	-----	-----						
<i>Centriscus teleajensis</i>					-----			-----	-----	-----						
<i>Clupea</i> sp.			-----	-----				-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Clupea sardinites</i>		-----		-----				-----	-----	-----						
<i>Diaphus</i> sp.								-----								
<i>Eomyctophum</i> sp.				-----				-----	-----	-----		-----				
<i>Eomyctophum limicola</i>				-----	-----			-----	-----	-----				-----	-----	-----
<i>Glossanodon</i> sp.								-----	-----	-----					-----	-----
<i>Lepidopus</i> sp.		-----		-----				-----	-----	-----					-----	-----
<i>Lepidopus glarisianus</i>				-----				-----	-----	-----						
<i>Palaeogadus</i> sp.				-----				-----	-----	-----						
<i>Palaeorhynchus</i> sp.					-----			-----	-----	-----		-----				
<i>Palimphyes</i> sp.		-----		-----				-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Palimphyes lanceolata</i>								-----	-----	-----						
<i>Polyipnus</i> sp.								-----								
<i>Scomber voitestii</i>								-----								
<i>Scopeloides</i> sp.				-----	-----			-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Scopeloides glarisianus</i>				-----				-----	-----	-----						
<i>Scorpaenoides</i> sp.								-----	-----	-----						
<i>Scorpaenoides popovicii</i>								-----	-----	-----						
<i>Serranus</i> sp.												-----				
<i>Syngnathus</i> sp.				-----				-----	-----	-----						
<i>Thyrsitoides</i> sp.								-----								
<i>Vinciguerra</i> sp.			-----	-----				-----	-----	-----	-----	-----	-----	-----	-----	-----
<i>Vinciguerra distincta</i>								-----	-----	-----						
<i>Vinciguerra obscura</i>				-----				-----	-----	-----						
<i>Vinciguerra talgiensis</i>			-----					-----	-----	-----						
<i>Zenopsis</i> sp.								-----								
<i>Zenopsis clarus</i>								-----								
<i>Cetorhinus</i> sp.		-----		-----				-----	-----	-----	-----	-----	-----	-----	-----	-----
Number of individuals		13	7	17	93	18	40	258	202	143	7	72	26	13	167	39



Ranks of taxa frequency refer to the following numbers of specimens

0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 22

Ichthyofaunal assemblages in exposures of the upper part of the Menilite Formation (above the Dynów Mbr) of inner tectonic units of the study area (columns: CH - W) and within the combined Rudawka, Futoma, and Borek Nowy members of the Skole Unit

Taxon \ Exposure	CH	WW	RR ₁₋₃	KL	RO ₁	R _{1,4}	BB	W	T ₁	D ₁	DG	H _{DS} ³⁻⁵	S _{1b} ³	HE HK ₁	P ₄	BN ³⁻⁵ BE ₁	L	M ₂	RB ₁₋₃	J _{D-G}	BZ BP ₁	ŚR	WE _{up}		
<i>Alosa</i> sp.																									
<i>Ammodytes</i> sp.																									
<i>Ammodytes antipai</i>																									
<i>Capros</i> sp.																									
<i>Capros radobojanus</i>																									
<i>Caranx</i> sp.																									
<i>Caranx petrodavae</i>																									
<i>Clupea</i> sp.																									
<i>Clupea sardinites</i>																									
<i>Eophycis</i> sp.																									
<i>Eophycis jamnensis</i>																									
<i>Fistularia</i> sp.																									
<i>Glossanodon</i> sp.																									
<i>Glossanodon musceli</i>																									
<i>Hemiramphus jerzyi</i>																									
<i>Hipposyngnathus neriticus</i>																									
<i>Holosteus</i> sp.																									
<i>Holosteus mariae</i>																									
<i>Leiognathus</i> sp.																									
<i>Lepidopus</i> sp.																									
<i>Lepidopus glarisianus</i>																									
<i>Merluccius</i> sp.																									
<i>Palaeogadus</i> sp.																									
<i>Palaeogadus abbreviatus</i>																									
<i>Palaeogadus simionescui</i>																									
<i>Palaeomolva</i> sp.																									
<i>Palaeorhynchus</i> sp.																									
<i>Palimphyes</i> sp.																									
<i>Pinichthys</i> sp.																									
<i>Pomolobus</i> sp.																									
<i>Properca</i> sp.																									
<i>Properca sabbai</i>																									
<i>Propercarina</i> sp.																									
<i>Sarda</i> sp.																									
<i>Scomber voitestii</i>																									
<i>Serranus</i> sp.																									
<i>Serranus budensis</i>																									
<i>Syngnathus</i> sp.																									
<i>Syngnathus incompletus</i>																									
<i>Trachinus</i> sp.																									
<i>Trachinus minutus</i>																									
Number of individuals	30	30	95	16	521	116	10	137	23	84	145	23	28	24	128	11	73	41	77	644	9	10	98		

----- 0 1 2 3 4 5 6 7 8 9

Ranks of taxa frequency refer to the following numbers of specimens

0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Variability of ichthyofaunal assemblages among the distinguished Palaeogene (IPM) and Neogene (INM) zones in the studied portion of the Carpathians

Taxon	Zone	IMP1	IMP2	IMP3	IMP4A	IMP4	IMP5	IMP6	IMP7	INM1
<i>Alosa</i> sp.										
<i>Clupea</i> sp.										
<i>Lepidopus</i> sp.										
<i>Syngnathus</i> sp.										
<i>Eomyctophum</i> sp.										
<i>Thyrsoideus</i> sp.										
<i>Vinciguerria distincta</i>										
<i>Serranus</i> sp.										
<i>Scorpaenoides</i> sp.										
<i>Vinciguerria</i> sp.										
<i>Palaeorhynchus</i> sp.										
<i>Palaeogadus</i> sp.										
<i>Polyipnus</i> sp.										
<i>Clupea sardinites</i>										
<i>Lepidopus glarisianus</i>										
<i>Capros radobojanus</i>										
<i>Caranx petrodavae</i>										
<i>Scomber voitestii</i>										
<i>Cetorhinus</i> sp.										
<i>Centriscus</i> sp.										
<i>Vinciguerria obscura</i>										
<i>Zenopsis</i> sp.										
<i>Zenopsis clarus</i>										
<i>Ammodytes antipai</i>										
<i>Palimphyes</i> sp.										
<i>Glossanodon</i> sp.										
<i>Centriscus heinrichi</i>										
<i>Centriscus longispinus</i>										
<i>Centriscus teleajensis</i>										
<i>Diaphus</i> sp.										
<i>Eomyctophum limicola</i>										
<i>Palimphyes lanceolata</i>										
<i>Scopeloides</i> sp.										
<i>Scopeloides glarisianus</i>										
<i>Scorpaenoides popovicii</i>										
<i>Barbus</i> sp.										
<i>Vinciguerria talgiensis</i>										
<i>Leiognathus</i> sp.										
<i>Merluccius</i> sp.										
<i>Syngnathus incompletus</i>										
<i>Fistularia</i> sp.										
<i>Caranx</i> sp.										
<i>Propercarina</i> sp.										
<i>Ammodytes</i> sp.										
<i>Palaeomolva</i> sp.										
<i>Pinichthys</i> sp.										
<i>Properca sabbai</i>										
<i>Serranus budensis</i>										
<i>Sarda</i> sp.										
<i>Holosteus</i> sp.										
<i>Capros</i> sp.										
<i>Properca</i> sp.										
<i>Palaeogadus simionescui</i>										
<i>Eophycis</i> sp.										
<i>Eophycis jamnensis</i>										
<i>Glossanodon musceli</i>										
<i>Hemiramphus jerzyi</i>										
<i>Hipposyngnathus neriticus</i>										
<i>Holosteus mariae</i>										
<i>Pomolobus</i> sp.										
<i>Trachinus</i> sp.										
<i>Trachinus minutus</i>										
<i>Palaeogadus abbreviatus</i>										
<i>Hemithyriscus</i> sp.										
<i>Echeneis carpathica</i>										
<i>Idrissia</i> sp.										
<i>Lepidopus isopleurus</i>										
<i>Apostasis</i> sp.										
<i>Priacanthus</i> sp.										
<i>Zeus</i> sp.										
<i>Hemithyriscus rumanus</i>										
<i>Polyipnus cf. anteasteroides</i>										
<i>Antigonia</i> sp.										
<i>Bregmaceros</i> sp.										
<i>Bregmaceros filamentosus</i>										
<i>Bathyprius</i> sp.										
<i>Kotlarczykia</i> sp.										
<i>Kotlarczykia bathybia</i>										
<i>Mugil</i> sp.										
<i>Polyipnus brevis</i>										
<i>Solenorhynchus</i> sp.										
<i>Eomyctophum cf. koraense</i>										
<i>Africentrus</i> sp.										
<i>Holocentroides</i> sp.										
<i>Psenicubiceps</i> sp.										
<i>Zeus faber</i>										
<i>Parahollardia ?</i> sp.										
<i>Syngnathus</i> sp. (typus A)										
<i>Onobrosomus</i> sp.										
<i>Carpathospinosus</i> sp.										
<i>Carpathospinosus propheticus</i>										
<i>Caprovesposus</i> sp.										
<i>Centriscus nov. sp.</i>										
<i>Forcipiger</i> sp.										
<i>Oligobalistes</i> sp.										
<i>Scorpaena</i> sp.										
<i>Pseudoranicus</i> sp.										
<i>Holocentroides moldavicus</i>										
<i>Eomyctophum mennis</i>										
<i>Vinciguerria merklini</i>										
<i>Alosa cf. sagorensis</i>										
<i>Palaeomolva monstrata</i>										
<i>Alopias</i> sp.										
<i>Equula ?</i> sp.										
<i>Idrissia carpathica</i>										
<i>Oligolactoria bubiki</i>										
<i>Polyipnus sobniowiensis</i>										
<i>Polyipnus cf. sobniowiensis</i>										
<i>Priacanthus longispinus</i>										
<i>Palaeogadus distinctus</i> n.sp.										
<i>Acanthocybium</i> sp.										
<i>Argyropelecus</i> sp.										
<i>Nessorhamphus</i> sp.										
<i>Carpathichthys</i> sp.										
<i>Carpathichthys polonicus</i>										
<i>Syngnathus</i> sp. (typus B)										
<i>Sphyraena</i> sp.										
<i>Glyptothorax</i> sp.										
<i>Palaeogadus intergerinus</i>										
<i>Parasteindachneria oligocaenica</i> n.sp.										
<i>Palaeogadus carpathicus</i> n.sp.										
<i>Argyropelecus cosmovicii</i>										
<i>Paraberyx bachoviensis</i> n. sp.										
<i>Paraberyx</i> gen. nov.										
<i>Archaeus</i> sp.										
<i>Capros medianus</i>										
<i>Prohollardia avita</i>										
<i>Protomyctophum</i> sp.										
<i>Propteridium</i> sp.										
<i>Notidanus</i> sp.										
<i>Caranx gracilis</i>										
<i>Leiognathus cf. minutus</i>										
<i>Merluccius errans</i>										
<i>Merluccius hartensis</i> n.sp.										
<i>Gobius</i> sp.										
Number of individuals		1096	2312	452	1234	792	601	3276	452	148
Clupeidae										
Scombridae										
Bathylagidae										
Bathylagidae (typus-"Melania")										
Gempylidae										
Gonostomatidae										
Sternoptychidae (typus-"xz")										
Brotulidae										
Gadidae										
Myctophidae										
Myctophidae (typus-"Giant-II")										
Sternoptychidae										
Trichiuridae										
Argentinidae										
Paralepididae										
Scorpaenidae										
Antennariidae										
Apogonidae										
Balistidae										
Thunninae										
Fistulariidae										
Aulorhynchidae										
Zeidae										
Triacanthodidae										
Aulostomidae										
Caproidae										
Nomeidae										
Nessoramphidae										
Psettopterygiidae										
Carangidae										
Alepocephalidae										
Ceratiidae										
Syngnathidae										
Echeneidae										
Moridae										
Berycidae										
Ostraciidae										
Trachichthyidae										
Number of individuals		117	46	98	210	71	94	371	45	4
Gadiformes										
Perciformes										
Beryciformes										
Salmoniformes? (typus-"xx")										
Pleuronectiformes										
Tetraodontiformes										
Clupeiformes										
Perciformes (typus-"à la, à la")										
Ophidiiformes										
Scorpaeniformes										
Anguilliformes										
Zeiformes										
Syngnathiformes										
Lamniiformes										
Salmoniformes										
Stomiiformes										
Number of individuals		26	65	35	56	21	43	102	11	20
Scombroidei										
Percoidei										
Stromateoidei										
Stromateoidei ? (typus-"Giant III")										
Trichiuroidei										
Number of individuals		2	7	8	10	4	10	31	1	2
Genus indet.										
Genus indet. (typus A)										
Genus indet. (typus P)										
Number of individuals		97	89	56	59	14	18			

Table 27

Spatial distribution of taxa of the IPM1 Zone assemblage throughout the study area zones

Taxon \ Area	VIII	VII	VI	V	IV	III	II	I
<i>Alosa</i> sp.	-----				-----			
<i>Ammodytes antipai</i>								-----
<i>Barbus</i> sp.					-----			
<i>Capros radobojanus</i>								-----
<i>Caranx petrodavae</i>								-----
<i>Centriscus</i> sp.				-----		-----	-----	-----
<i>Centriscus heinrichi</i>				-----				-----
<i>Centriscus longispinus</i>				-----			-----	-----
<i>Centriscus teleajensis</i>					-----			-----
<i>Clupea</i> sp.	-----			-----	-----		-----	-----
<i>Clupea sardinites</i>	-----			-----	-----		-----	-----
<i>Diaphus</i> sp.							-----	-----
<i>Eomyctophum</i> sp.			-----	-----			-----	-----
<i>Eomyctophum limicola</i>				-----	-----		-----	-----
<i>Glossanodon</i> sp.					-----		-----	-----
<i>Glossanodon musceli</i>					-----		-----	-----
<i>Lepidopus</i> sp.	-----		-----		-----		-----	-----
<i>Lepidopus glarisanus</i>				-----		-----		-----
<i>Palaeogadus</i> sp.								-----
<i>Palaeorhynchus</i> sp.			-----		-----		-----	-----
<i>Palimphyes</i> sp.	-----		-----	-----	-----		-----	-----
<i>Palimphyes lanceolata</i>								-----
<i>Polyipnus</i> sp.							-----	-----
<i>Scomber voitestii</i>								-----
<i>Scopeloides</i> sp.	-----		-----	-----	-----		-----	-----
<i>Scopeloides glarisanus</i>								-----
<i>Scorpaenoides</i> sp.					-----			-----
<i>Scorpaenoides popovicii</i>							-----	-----
<i>Serranus</i> sp.			-----					-----
<i>Syngnathus</i> sp.					-----		-----	-----
<i>Thyrsitoides</i> sp.							-----	-----
<i>Vinciguerra</i> sp.			-----		-----		-----	-----
<i>Vinciguerra distincta</i>					-----		-----	-----
<i>Vinciguerra obscura</i>				-----			-----	-----
<i>Vinciguerra talgiensis</i>				-----				-----
<i>Zenopsis</i> sp.								-----
<i>Zenopsis clarus</i>								-----
<i>Cetorhinus</i> sp.	-----		-----	-----	-----			-----

0 1 2 3 4 5 6 7 8 9

Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 28

Spatial distribution of taxa of the IPM2 Zone assemblage throughout the study area zones

Taxon \ Area	VIII	VII	VI	V	IV	III	II	I
<i>Alosa</i> sp.								
<i>Ammodytes</i> sp.					6			
<i>Ammodytes antipai</i>	1			5				
<i>Antigonia</i> sp.		4						
<i>Capros</i> sp.					4		4	
<i>Capros radobojanus</i>	3			1				
<i>Caranx</i> sp.				4				
<i>Caranx petrodavae</i>	4		4					
<i>Clupea</i> sp.	3		5	6	7	8	8	
<i>Clupea sardinites</i>	3		5	6				9
<i>Eophycis</i> sp.	4			4			4	
<i>Eophycis jamnensis</i>	4			1				9
<i>Fistularia</i> sp.				4				
<i>Glossanodon</i> sp.			5	6	7		8	
<i>Glossanodon musceli</i>	3		5	6		4		9
<i>Hemiramphus jerzyi</i>				4				
<i>Hemithysites</i> sp.				4				4
<i>Hipposyngnathus neriticus</i>								9
<i>Holosteus</i> sp.				4	6			
<i>Holosteus mariae</i>	4							
<i>Leiognathus</i> sp.	4							
<i>Lepidopus</i> sp.				1			1	9
<i>Lepidopus glarisanus</i>	4			1				9
<i>Merluccius</i> sp.					1	4		
<i>Palaeogadus</i> sp.	3		5	6	7			
<i>Palaeogadus abbreviatus</i>								4
<i>Palaeogadus simionescui</i>	3	4	5	6				9
<i>Palaeomolva</i> sp.							4	
<i>Palaeorhynchus</i> sp.	4					4		
<i>Palimphyes</i> sp.	4							
<i>Pinichthys</i> sp.			1					
<i>Pomolobus</i> sp.	4			1				
<i>Properca</i> sp.						4		
<i>Properca sabbai</i>	3							
<i>Propercarina</i> sp.	4							1
<i>Sarda</i> sp.	4		4					
<i>Scomber voitestii</i>								
<i>Serranus</i> sp.	3	4	5	6	7		8	
<i>Serranus budensis</i>	3		5	6			4	9
<i>Syngnathus</i> sp.								1
<i>Syngnathus incompletus</i>	4							1
<i>Trachinus</i> sp.	4-?						4-?	1
<i>Trachinus minutus</i>				4				9

0 1 2 3 4 5 6 7 8 9

Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 29

Spatial distribution of taxa of the IPM3 Zone assemblage throughout the study area zones

Taxon \ Area	VIII	VII	VI	V	IV	III	II	I
<i>Alosa</i> sp.				-----				
<i>Apostasis</i> sp.		=====						
<i>Bathyprion</i> sp.						-----		
<i>Bregmaceros</i> sp.		=====						
<i>Bregmaceros filamentosus</i>		=====				=====		
<i>Clupea</i> sp.		=====		-----		=====		
<i>Clupea sardinites</i>						=====		
<i>Echeneis carpathica</i>		=====						
<i>Eomyctophum</i> sp.		-----				=====		
<i>Hemithysites</i> sp.						=====		
<i>Hemithysites rumanus</i>						-----		
<i>Idrissia</i> sp.		-----				-----		
<i>Kotlarczykia</i> sp.		=====						
<i>Kotlarczykia bathybia</i>		-----		=====		=====		
<i>Lepidopus</i> sp.		=====		=====		=====		
<i>Lepidopus isopleurus</i>				=====				
<i>Mugil</i> sp.				-----				
<i>Palaeogadus</i> sp.		=====						
<i>Palaeomolva</i> sp.		-----						
<i>Palaeorhynchus</i> sp.		=====		-----				
<i>Polyipnus</i> sp.		=====						
<i>Polyipnus brevis</i>		=====		=====		=====		
<i>Polyipnus</i> cf. <i>anteasteroides</i>						=====		
<i>Priacanthus</i> sp.		-----						
<i>Properca</i> sp.		-----						
<i>Propercarina</i> sp.		-----						
<i>Scorpaenoides</i> sp.		-----				-----		
<i>Serranus</i> sp.		=====						
<i>Solenorhynchus</i> sp.						-----		
<i>Syngnathus</i> sp.		=====						
<i>Thyrsitoides</i> sp.						=====		
<i>Vinciguerra</i> sp.				-----		=====		
<i>Vinciguerra distincta</i>						=====		
<i>Zenopsis</i> sp.		=====				-----		
<i>Zenopsis clarus</i>				-----				
<i>Zeus</i> sp.		=====						

0 1 2 3 4 5 6 7 8 9

Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 30

Spatial distribution of taxa of the IPM4 and IPM4A (marked by apostrophe)
Zone assemblage throughout the study area zones

Taxon \ Area	VIII	VII	VII'	VI	V	IV	III	II	I	I'
<i>Africentrum</i> sp.	-----						-----			
<i>Alosa</i> sp.			-----				-----			
<i>Alosa</i> cf. <i>sagorensis</i>							-----			
<i>Apostasis</i> sp.							-----			
<i>Clupea</i> sp.		-----	-----		-----	-----	-----			
<i>Clupea sardinites</i>	-----			-----			-----		-----	
<i>Echeneis carpathica</i>							-----			
<i>Eomyctophum</i> sp.	-----	-----		-----			-----			
<i>Eomyctophum</i> cf. <i>koraense</i>	-----						-----			-----
<i>Eomyctophum menneri</i>	-----	-----				-----				
<i>Equula?</i> sp.	-----									
<i>Hemithysites</i> sp.			-----							
<i>Holocentroides moldavicus</i>						-----	-----		-----	
<i>Holocentroides</i> sp.		-----	-----				-----		-----	
<i>Holosteus</i> sp.	-----						-----			
<i>Idrissia</i> sp.		-----	-----				-----			
<i>Idrissia carpathica</i>	-----					-----				
<i>Lepidopus</i> sp.			-----	-----			-----		-----	
<i>Merluccius</i> sp.	-----			-----			-----			
<i>Oligolactoria bubiki</i>									-----	
<i>Palaeogadus</i> sp.	-----									
<i>Palaeomolva monstrata</i>							-----			
<i>Palaeorhynchus</i> sp.			-----				-----			
<i>Polyipnus</i> sp.	-----	-----	-----			-----				
<i>Polyipnus</i> cf. <i>anteasteroides</i>	-----						-----			
<i>Polyipnus sobnioviensis</i>	-----	-----				-----				
<i>Polyipnus</i> cf. <i>sobnioviensis</i>	-----			-----			-----			
<i>Priacanthus</i> sp.	-----						-----			
<i>Priacanthus longispinus</i>						-----				
<i>Sarda</i> sp.	-----					-----				
<i>Scomber voitestii</i>			-----				-----			
<i>Scorpaenoides</i> sp.			-----				-----			
<i>Serranus</i> sp.			-----				-----			
<i>Syngnathus</i> sp.			-----				-----			
<i>Syngnathus incompletus</i>							-----			-----
<i>Thyrsitoides</i> sp.			-----				-----			
<i>Vinciguerria</i> sp.					-----		-----			
<i>Vinciguerria merklini</i>					-----		-----			
<i>Vinciguerria obscura</i>					-----		-----			
<i>Zeus</i> sp.			-----				-----			
<i>Zeus faber</i>			-----				-----			
<i>Alopecias</i> sp.						-----				
<i>Cetorhinus</i> sp.							-----			
Nessoramphidae							-----			

<i>Antigonia</i> sp.			-----							
<i>Bregmaceros</i> sp.			-----							
<i>Bregmaceros filamentosus</i>			-----							
<i>Capros</i> sp.			-----							
<i>Capros radobojanus</i>			-----							
<i>Caprovesposus</i> sp.			-----							
<i>Carpathospinosus</i> sp.			-----							
<i>Carpathospinosus propheticus</i>			-----							
<i>Centriscus</i> sp.			-----							
<i>Centriscus</i> nov. sp.			-----							
<i>Fistularia</i> sp.			-----							
<i>Forcipiger</i> sp.										-----
<i>Oligobalistes</i> sp.			-----							
<i>Onobrosmius</i> sp.			-----							
<i>Parahollardia ?</i> sp.			-----							
<i>Psenicubiceps</i> sp.			-----							
<i>Pseudoraniceps</i> sp.			-----							
<i>Scorpaena</i> sp.			-----							
<i>Syngnathus</i> sp. (typus A)			-----							
<i>Zenopsis</i> sp.			-----							



Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 31

Spatial distribution of taxa of the IPM5 Zone assemblage throughout the study area zones

Taxon	Area	VIII	VII	VI	V	IV	III	II	I
<i>Africentrum</i> sp.				██			██		
<i>Alosa</i> sp.				██			██		
<i>Apostasis</i> sp.				██			██		
<i>Carpathichthys</i> sp.				██			██		
<i>Carpathichthys polonicus</i>				██			██		
<i>Clupea</i> sp.		██	██	██			██		
<i>Clupea sardinites</i>				██			██		
<i>Eomyctophum</i> sp.			---	██			██		
<i>Hemithyrsites</i> sp.				██			██		
<i>Holocentroides moldavicus</i>				██			██		
<i>Holocentroides</i> sp.			---	██			██		
<i>Idrissia</i> sp.			██	██			██		
<i>Lepidopus</i> sp.			██	██			██		
<i>Palaeorhynchus</i> sp.				██			██		
<i>Pinichthys</i> sp.				██			██		
<i>Psenicubiceps</i> sp.			---	██			██		
<i>Sarda</i> sp.				██			██		
<i>Scomber voitestii</i>				██			██		
<i>Scorpaenoides</i> sp.				██			██		
<i>Serranus</i> sp.				██			██		
<i>Syngnathus</i> sp.				██			██		
<i>Syngnathus</i> sp. (typus B)			██	██			██		
Alepocephalidae			██	██			██		
<i>Acanthocybium</i> sp.							---		
<i>Argyrolepecus</i> sp.							---		
<i>Caranx petrodavae</i>							---		
<i>Centriscus</i> sp.							---		
<i>Cetorhinus</i> sp.							---		
<i>Echeneis carpathica</i>							---		
<i>Kotlarczykia</i> sp.							---		
<i>Merluccius</i> sp.							---		
<i>Nessoramphus</i> sp.							---		
<i>Palaeogadus distinctus</i> n.sp.							---		
<i>Polyipnus</i> cf. <i>anteasteroides</i>							---		
<i>Polyipnus</i> sp.							---		
<i>Priacanthus</i> sp.							---		
<i>Sphyraena</i> sp.							---		
<i>Syngnathus</i> sp. (typus A)							██		
<i>Vinciguerria</i> sp.							██		
<i>Zeus</i> sp.							██		



Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 32

Spatial distribution of taxa of the IPM6 Zone assemblage throughout the study area zones

Taxon	Area	VIII	VII	VI	V	IV	III	II	I
<i>Acanthocybium</i> sp.						-----			
<i>Africentrum</i> sp.			=====			-----			
<i>Alosa</i> sp.			=====		-----	=====			-----
<i>Alosa</i> cf. <i>sagorensis</i>									
<i>Ammodytes</i> sp.									
<i>Antigonia</i> sp.			-----			-----			
<i>Apostasis</i> sp.						-----			
<i>Archaeus</i> sp.									
<i>Argyrolepecus</i> sp.			=====	-----		=====	=====	=====	
<i>Argyrolepecus cosmovicii</i>								=====	
<i>Capros medianus</i>								-----	
<i>Capros radobojanus</i>								-----	
<i>Caranx</i> sp.						-----			
<i>Caranx petrodavae</i>							-----		
<i>Clupea</i> sp.			=====		=====	=====	=====	=====	-----
<i>Clupea sardinites</i>								=====	
<i>Echeneis carpathica</i>									
<i>Eomyctophum</i> sp.			=====	=====	=====	=====	-----	=====	-----
<i>Eomyctophum</i> cf. <i>koraense</i>								-----	
<i>Eomyctophum menneri</i>								-----	
<i>Glyptophidium</i> sp.			-----						
<i>Hemithysites</i> sp.			-----			=====	=====		
<i>Hemithysites rumanus</i>							-----		
<i>Holocentroides moldavicus</i>									
<i>Holocentroides</i> sp.								-----	
<i>Idrissia</i> sp.						=====	=====		
<i>Lepidopus</i> sp.			=====		-----	=====	=====	-----	-----
<i>Lepidopus glarisanus</i>								-----	
<i>Lepidopus isopleurus</i>								-----	
<i>Merluccius</i> sp.			=====			=====	=====		
<i>Nessorhamphus</i> sp.									
<i>Onobrosmius</i> sp.									
<i>Palaeogadus</i> sp.						-----			
<i>Palaeogadus carpathicus</i> n.sp.							-----		
<i>Palaeogadus distinctus</i> n.sp.			=====			=====	=====	-----	
<i>Palaeogadus intergerinus</i>						=====		-----	
<i>Palaeomolva</i> sp.									
<i>Palaeomolva monstrata</i>							-----		
<i>Palaeorhynchus</i> sp.			=====						
<i>Paraberyx bachoviensis</i> n.sp.								-----	
<i>Paraberyx</i> gen. nov.								-----	
<i>Parahollandia</i> ? sp.						-----			
<i>Parasteindachneria oligocaenica</i> n.sp.								-----	
<i>Pinichthys</i> sp.								-----	
<i>Polyipnus</i> sp.			-----						
<i>Priacanthus</i> sp.			-----		-----		-----		
<i>Prohollandia avita</i>						-----			
<i>Properca sabbai</i>								-----	
<i>Propercarina</i> sp.								-----	
<i>Propteridium</i> sp.								-----	
<i>Protomyctophum</i> sp.									
<i>Psenicubiceps</i> sp.									
<i>Scomber voitestii</i>								-----	
<i>Scorpaenoides</i> sp.			=====					-----	
<i>Serranus</i> sp.					-----	=====	=====		
<i>Serranus budensis</i>								-----	
<i>Syngnathus</i> sp.					-----	=====	-----		
<i>Syngnathus</i> sp. (typus A)								-----	
<i>Syngnathus incompletus</i>			=====	-----				=====	
<i>Thyrstitoides</i> sp.								=====	
<i>Vinciguerria</i> sp.						=====	=====		
<i>Vinciguerria distincta</i>					-----			-----	
<i>Vinciguerria merklini</i>								-----	
<i>Zeus</i> sp.								-----	
<i>Zeus faber</i>								-----	
Alepocephalidae			-----					-----	

----- 0 1 2 3 4 5 6 7 8 9

Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 33

Spatial distribution of taxa of the IPM7 Zone assemblage throughout the study area zones

Taxon \ Area	VIII	VII	VI	V	IV	III	II	I
<i>Africentrum</i> sp.				-----				
<i>Alosa</i> sp.					-----			
<i>Caranx</i> sp.						-----		
<i>Clupea</i> sp.			-----	████████	████████	████████	████████	-----
<i>Echeneis carpathica</i>				-----	-----			
<i>Eomyctophum</i> sp.			-----	████████	████████	████████	████████	-----
<i>Eomyctophum</i> cf. <i>koraense</i>					-----	-----		-----
<i>Eomyctophum menneri</i>						-----	-----	
<i>Fistularia</i> sp.				-----				
<i>Glyptophidium</i> sp.				-----				
<i>Hemithysites</i> sp.				-----		-----	-----	
<i>Holocentroides moldavicus</i>				-----				
<i>Idrissia</i> sp.				████████	-----			
<i>Lepidopus</i> sp.					-----	████████	-----	-----
<i>Lepidopus isopleurus</i>					-----			
<i>Merluccius</i> sp.			-----	████████	████████	████████	████████	
<i>Palaeogadus carpathicus</i> n.sp.						-----	-----	
<i>Palaeogadus distinctus</i> n.sp.					-----			
<i>Palaeogadus intergerinus</i>					-----			
<i>Palaeorhynchus</i> sp.						-----	-----	
<i>Parasteindachneria oligocaenica</i> n.sp.					-----			
<i>Scorpaenoides</i> sp.					-----			
<i>Serranus</i> sp.						-----	-----	
<i>Syngnathus</i> sp.				████████	████████	████████	████████	████████
<i>Syngnathus incompletus</i>			-----					
<i>Thyrsitoides</i> sp.				-----			-----	
<i>Vinciguerra</i> sp.					-----	-----		
<i>Vinciguerra distincta</i>							-----	-----
<i>Notidanus</i> sp.				-----				



Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800

Table 34

Spatial distribution of taxa of the INM1 Zone assemblage throughout the study area zones

Taxon \ Area	VIII	VII	VI	V	IV	III	II	I
<i>Alosa</i> sp.					—			
<i>Caranx gracilis</i>				---	—			
<i>Clupea</i> sp.				—	■			
<i>Gobius</i> sp.					---			
<i>Leiognathus</i> sp.					—			
<i>Leiognathus</i> cf. <i>minutus</i>					■			
<i>Lepidopus</i> sp.					—			
<i>Merluccius</i> sp.				---				
<i>Merluccius errans</i>				—	—			
<i>Merluccius hartensis</i> n.sp.					—			
<i>Syngnathus</i> sp.				—	—			



Ranks of taxa frequency refer to the following numbers of specimens: 0 = 1; 1 = 2-5; 2 = 6-10; 3 = 11-20; 4 = 21-50; 5 = 51-100; 6 = 101-200; 7 = 201-400; 8 = 401-800; 9 = >800