Taphonomy of ichthyofauna from an Oligocene sequence (Tylawa Limestones horizon) of the Outer Carpathians, Poland

Małgorzata BIEŃKOWSKA

Oligocene deposits at Rudawka Rymanowska (Silesian Nappe, Polish Outer Carpathians) contain abundant fish remains. Sandstones and shales, displaying features of low-density turbidity-current deposits, contain isolated fish bones and scales segregated as detrital elements. Fish skeletons occur in laminated Tylawa Limestones (taphonomic Assemblage A), considered to be pelagic in origin, and in laminated claystones (taphonomic Assemblage B), probably also pelagic. Assemblage A contains very well preserved skeletons; Assemblage B contains only 40 to 60% of well preserved skeletons, the rest being partially disintegrated. The very good state of preservation of skeletons in the Tylawa Limestones indicates cessation of decay soon after death. In the claystones, the fish carcasses had arrived at the sea floor in various stages of soft tissue decay, and the carcasses rested on the sea floor for variable lengths of time. Deformations of the vertebral columns in all specimens studied are considered to be natural post-mortem ones. Taphonomic analysis supplements sedimentary data to reconstruct an array of physical/biogenic agents and events that acted intermittently at the Oligocene sea floor in other parts of the Carpathians and of the Caucasus.

INTRODUCTION

A rich ichthyofauna has long been well known from the Menilite Beds of the Oligocene section of the Outer Carpathians in Poland (Rychlicki, 1909; Böhm, 1930; Jerzmańska, 1960, 1967, 1968; Jerzmańska and Kotlarczyk, 1968, 1976, 1991; Kotlarczyk and Jerzmańska, 1976, 1988; Szymczyk, 1978; Świdnicki, 1986, 1988). The subject of this paper is the taphonomy of fish skeletons from one locality (Rudawka Rymanowska in the Silesian Nappe, see Fig. 1), and its significance as regards the origin of all fish-bearing beds in the Carpathian sequence.

MATERIAL AND METHODS

The deposits studied were classified into the facies distinguished by Pickering *et al.* (1986) and to the divisions of the Bouma sequence (Bouma, 1962). The biostratonomic terminology used was after Kidwell *et al.* (1986).

The material contains 240 skeletons, which were collected in the exposures RU 01, RU 02, RU 03 between 1998 and 2001. Detailed taphonomic analyses have been carried out on four beds (WAP 2, WAP 1, 32, 34 — see Fig. 2). Each of these beds yielded 31 to 62 skeletons. Some observations could not be obtained for some incomplete specimens. The incompleteness of a specimen did not exclude it if the key feature for an analysis was preserved, leading to a different number of specimens for each analysis. The specimens are in the collection of the Institute of Geology, University of Warsaw.

EXAMINED SECTION

The Rudawka Rymanowska locality is situated 20 km SW of Krosno in the southern part of the Silesian Nappe. The research has been done at three exposures: two are in the Wisłok River valley and one in its tributary stream (see Fig. 1C). In all these exposures, the same upper part of the Menilite Beds is exposed, including two correlation horizons of the laminated Tylawa Limestones (Oligocene in age — see Fig. 1D). The
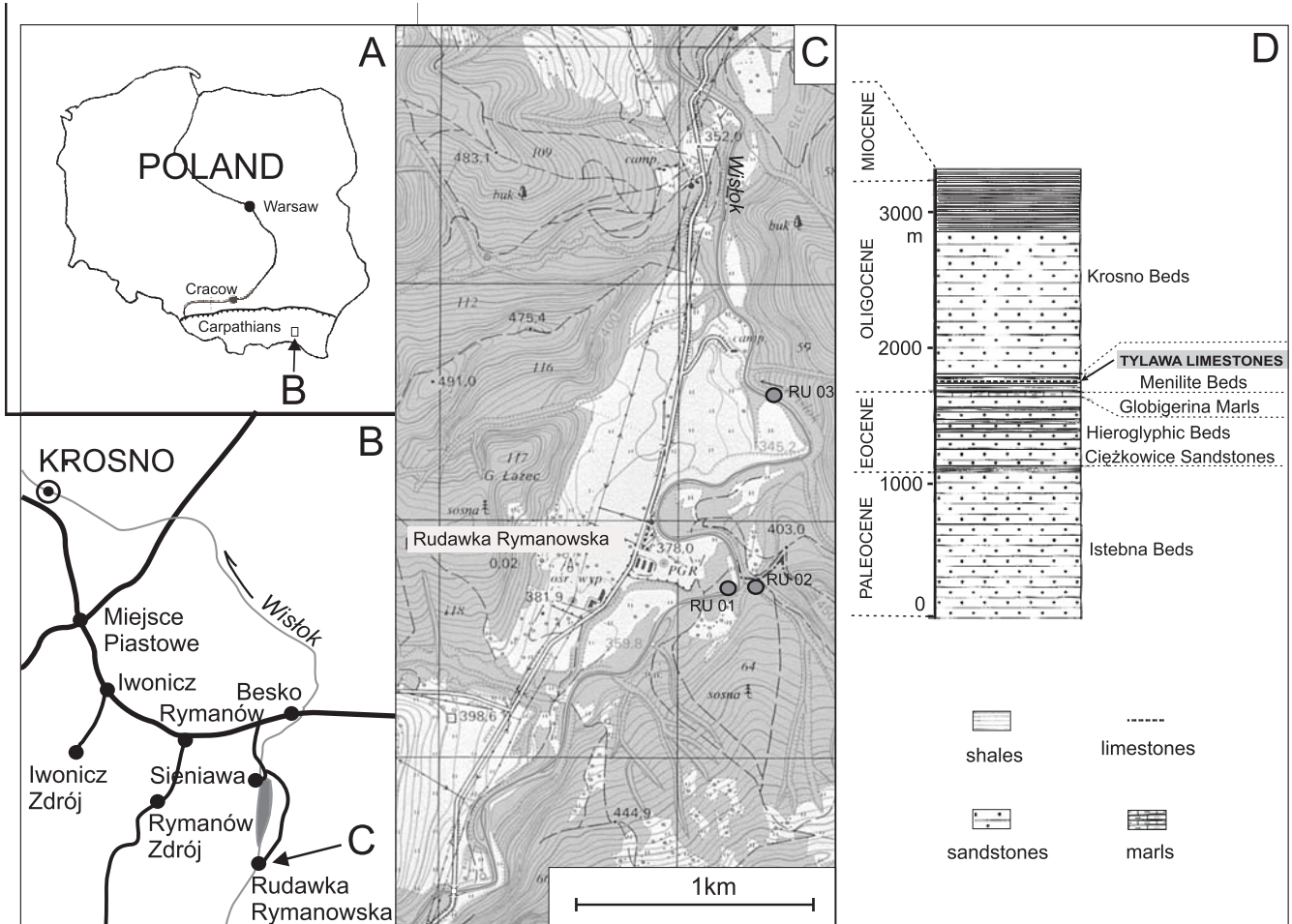
Fig. 1. A–C — locality map (RU 01, RU 02, RU 03 — fish-bearing exposures); D — simplified stratigraphy of Paleocene-Miocene deposits in the Silesian Nappe (adopted from Mastella and Konon, 2002)

sedimentology of the exposure RU 03 was analysed (Fig. 2). All the fish-bearing beds are also recognisable in the exposures RU 02 and RU 01.

The section examined (Fig. 2), appearing in all the three exposures, is composed mainly of dark grey or black non-laminated shales (claystones, mudstones, and siltstones), with a small proportion of fine-grained sandstones. Rarely, there also occur laminated claystones and limestones (laminated and non-laminated type of the Tylawa Limestones).

Grey, fine-grained sandstone beds display either sharp flat or load-casted soles, and they pass upwards into shales. The sandstones often display current ripple lamination, parallel lamination, and barely visible upward gradation of grain size. The upper surfaces of sandstone beds usually are gradual. The thickness of sandstones range from 0.1 to 20 cm; the thicker beds are distinct in each of the exposures, whereas very thin ones may locally disappear. The orthoquartzites studied display features of the $T_{c–d}$ divisions of the Bouma sequence and represent facies C2.3 of Pickering *et al.* (1986).

Dark grey to black shales (claystones, mudstones, and siltstones) occur in several millimetres-thick laminae to several centimetres-thick layers. The soles of the mudstones and siltstones locally comprise laminae of larger quartz grains. The layers underlain by sandstone usually show gradual bottom contacts. The layers underlain by limestone or by shale of an-

other type show distinctly flat or gradual bottom contacts. The shales display a distinctive bedding-parallel alignment of elongated particles (fish scales and bones, mica flakes); locally they contain up to 50% of peloids.

Some layers with peloids and indistinct lamination, up to 2 cm thick, contain abundant fish remains, including complete skeletons. On the bedding plane there is no preferred direction of skeletons, and disintegrated elements rest nearby. In the section studied, claystones, sandy claystones and silty claystones (see Picard, 1971) dominate over mudstones and siltstones. The shales display features of $T_{d–e}$ divisions of the Bouma sequence, and represent facies D2.1, D2.3, E1.1, E2.1, and E2.2 of Pickering *et al.* (1986).

Non-laminated limestones, light brown and light grey in colour occur in 2–8 cm thick layers. The soles and tops are gradual or distinctly flat. There are no primary sedimentary structures. The limestones studied display features typical of micrite (see Folk, 1959) and represent facies G1.2 of Pickering *et al.* (1986).

Laminated limestones occur in layers up to 3 cm thick. There are two kinds of laminae in the limestones: light, built of micrite, and dark, containing clay minerals and organic matter (Haczewski, 1989). The layers underlain by laminated claystones show gradual soles. The layers underlain by non-laminated limestone show distinctly flat soles. Tops of
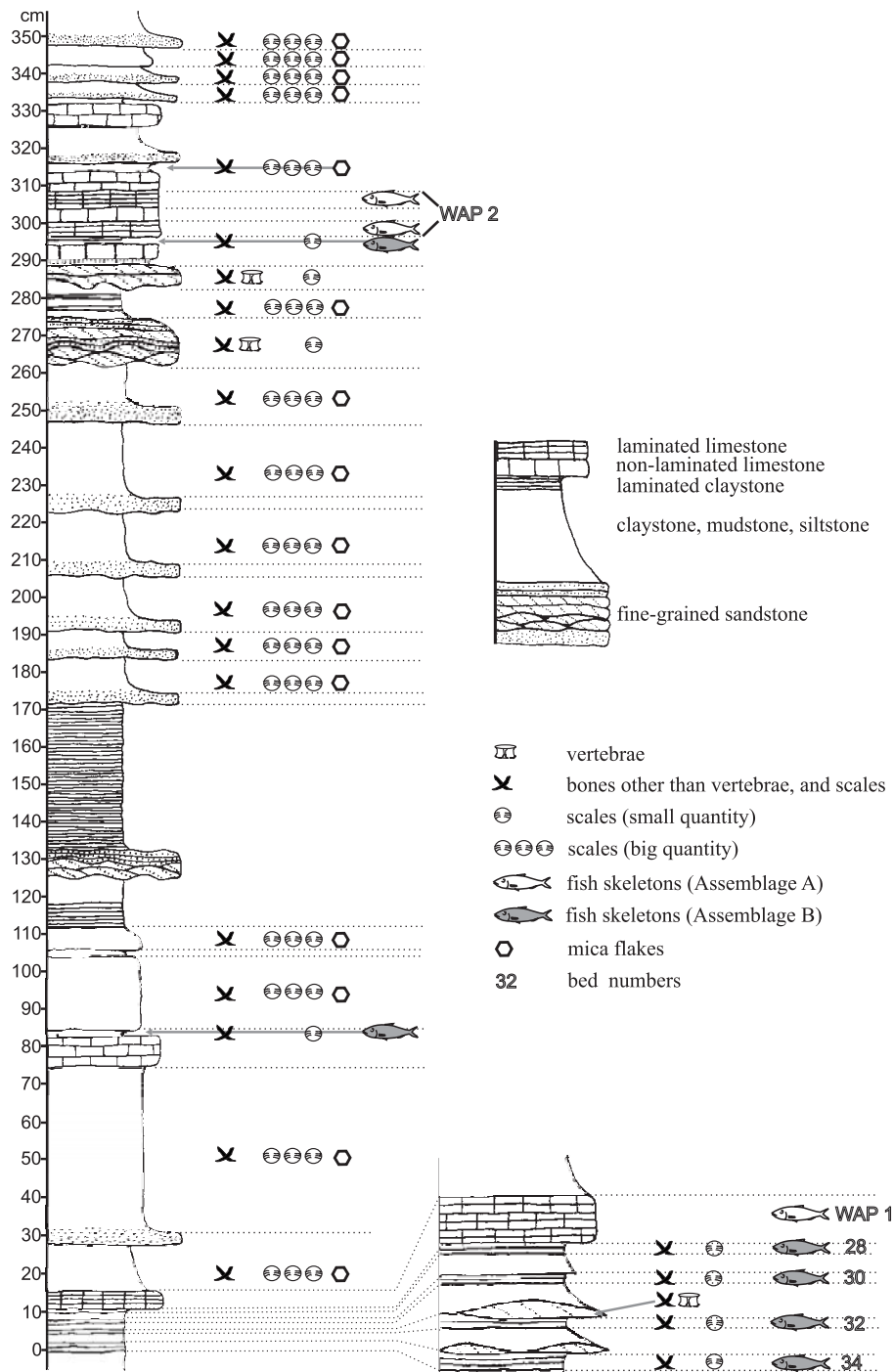
Fig. 2. Occurrence of fish remains in the section studied at Rudawka Rymanowska

the layers are distinctly flat. The laminated limestones contain fish skeletons. The limestones display features typical of micrite (see Folk, 1959) and represent facies G1.2 of Pickering *et al.* (1986).

In the section examined many turbidite layers were distinguished, comprising sandstones and shales, with features characteristic of Bouma's T_{c-e}, T_{d-e} and T_e sequences and of low-concentration turbidity-current deposits (see Stow and Piper, 1984; Pickering *et al.*, 1986). The laminated limestones are thought to be pelagic (Jucha, 1969; Haczewski, 1989). Within the laminated claystones, randomly dispersed skeletal elements rest in proximity to the rest of the skeleton, and the skeletons do not show preferred direction on the bedding plane, which indicates that these deposits could also be pelagic.

TAPHONOMY

Fish remains occur within various lithologies in the section studied (see Fig. 2). Some sandstone and siltstone beds contain bones and scales, whose sizes range up to 10 mm. Vertebrae

dominate in these beds over other bones and scales. Larger elements are located usually at the soles of beds. Fish remains occurring in laminated parts of beds are smaller than those at the soles. Clayey mudstones, silty claystones, and sandy claystones contain small scales and thin flat bones, commonly associated with mica flakes, and they display a distinctive parallel alignment of fish remains and mica flakes. Fish remains are uniformly dispersed in the deposit, but their quantity and size usually decrease upwards in the layers together with a decrease in the quantity and size of quartz grains and mica flakes. Isolated fish remains are segregated, as are other detrital elements. Non-laminated claystones and non-laminated limestones do not contain fish remains. Laminated claystones contain fish remains, partially disarticulated skeletons and complete skeletons. Laminated limestones contain well-preserved skeletons.

TAPHONOMY OF FISH SKELETONS

Concerning the taphonomy of fish skeletons, two taphonomic assemblages have previously been distinguished by the author (Bieńkowska, 2002). In Assemblage A, very well preserved skeletons dominate. Assemblage B contains 40–60% of well preserved skeletons, and the rest are partially disintegrated (see Fig. 3).

TYPICAL FEATURES OF ASSEMBLAGES

The two assemblages are polyspecific, containing several species each, but their taxonomic composition differs (Fig. 4). Fish skeletons occur in thin beds a few centimetres-thick, where the orientation of skeletons is concordant with bedding, and their packing is matrix supported. Along the bedding surfaces the skeletons are scattered. The orientations and directions of the skeletons were measured (Fig. 5) and both the χ^2 and the Rayleigh test (Davis, 1986) showed that the departure from a completely random orientation was statistically insignificant (2.914 df=5 α=0.05; mean R=0.12, n=31).

The skeletons are strongly compacted within the enclosing sediment. Bones and scales are well preserved; their colour is pale to dark brown. No remains of benthic organisms are present and there are no signs of carcasses penetrating into the sedi-

Fig. 4. Frequency of fish families in distinguished assemblages: Assemblage A — beds WAP 2 and WAP 1, Assemblage B — beds 32 and 34, total frequency in beds 28–34, numbers — quantity of specimens
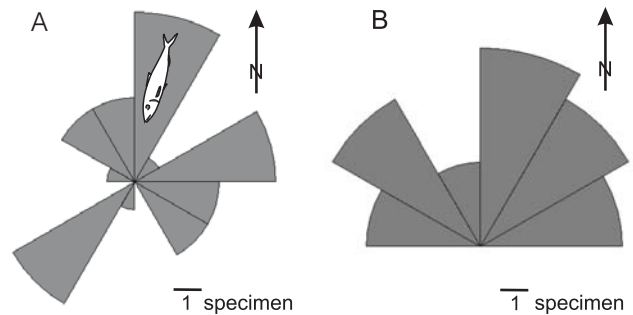
Fig. 5. Directions and orientations of skeletons in bed 34 in the exposure RU 03 (sample — 31 specimens): A — directions, B — orientations

ment, which remains undisturbed. Some signs of bacterial and chemical decomposition of soft parts of the fish body are recognisable. Apparent deformations of axial skeletons comprise S-shaped, arched, or broken vertebral columns.

ASSEMBLAGE A

Specimens of three species of the families Clupeidae, Argentinidae, and Serranidae occur in this assemblage. Body sizes are small: Clupeidae 2.5–10 cm, Argentinidae 3–6 cm, Serranidae 2.5–4.5 cm. Usually, fish lie either on the left or on the right side of the body, but in a few instances only a part of
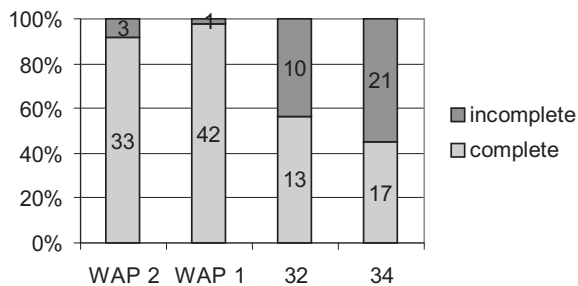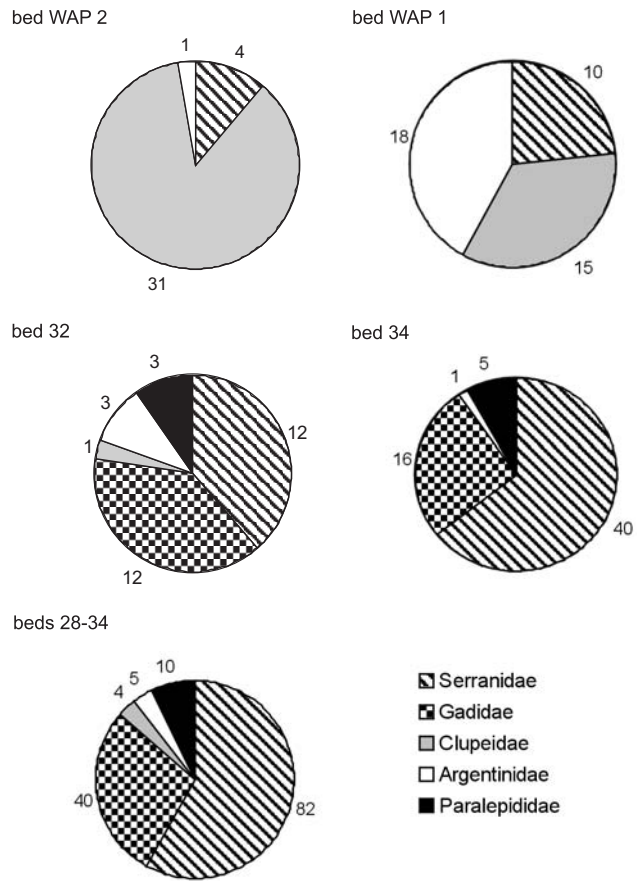

Fig. 3. Complete/incomplete skeleton ratio in beds WAP 1 and WAP 2 (Assemblage A), and in beds 32 and 34 (Assemblage B); numbers denote quantity of specimens

the body lies on its side, the rest being either flattened dorso-ventrally, or placed obliquely to the symmetry plane. Some bodies lay with their symmetry plane at an oblique angle to the bedding plane, as is shown in their fossilized state by their dorsal, ventral and anal fins being off the axis of symmetry but within the area enclosed by the outline (Fig. 6).

The skeletons are variably deformed, characteristically for the given families as follows (Fig. 11): the Argentinidae tend to

Fig. 9. Number of skeletons with jaws closed and gaped in beds WAP 1 and WAP 2 (Assemblage A), and in beds 32 and 34 (Assemblage B); numbers — quantity of specimens
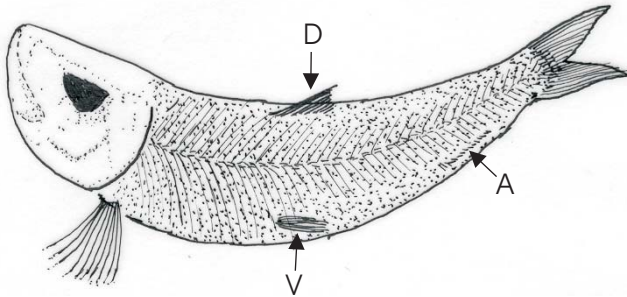

Fig. 6. A clupeid skeleton which lied with its symmetry plane at an oblique angle to the bedding plane, what is shown in its fossilized state by its dorsal, ventral and anal fins being off the axis of symmetry but enclosed by the outline; A — anal fin, D — dorsal fin, V — ventral fin

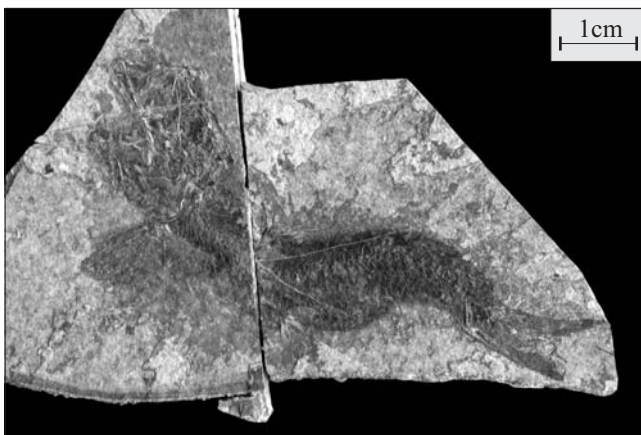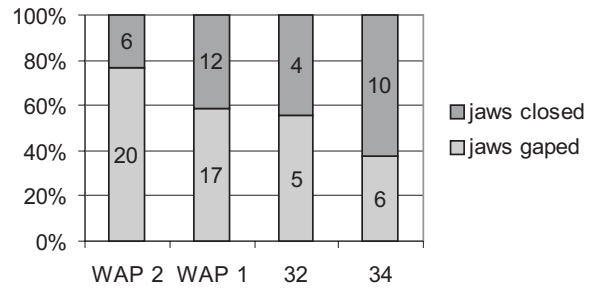Fig. 7. An argentinid skeleton (RU 03. WAP 1.14.) slightly arched; from bed WAP 1

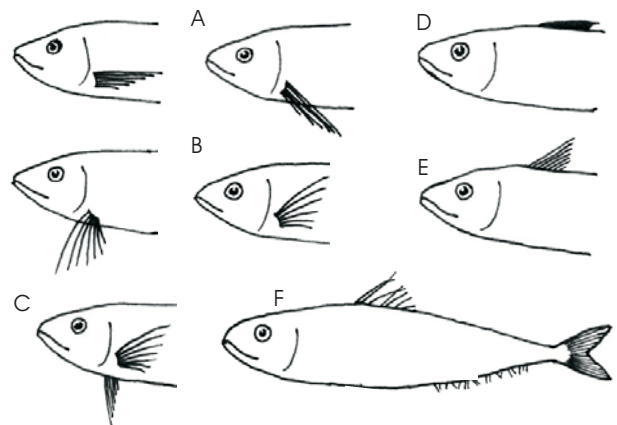Fig. 8. A clupeid skeleton (RU 03. WAP 1.33.), twisted in an S-shape; from bed WAP 1

Fig. 10. Distinguished setting of fins: A–C — pectoral fins (including pelvic fin), A — rays close one to another, B — rays flabellate, C — one fin has rays close one to another, but the other has rays flabellate; D — dorsal fin (including anal fin), rays close one to another and reclined close to the dorsal body outline; E — dorsal fin (including anal fin), rays set obliquely to the dorsal body outline; F — dorsal and anal fin have rays set disorderly

be slightly arched (73% of specimens; Fig. 7), and those with straight, S-shaped, or with broken vertebral columns are very rare; the Clupeidae are usually arched (54% of specimens; Fig. 15) or S-shaped (32% of specimens; Fig. 8), with all transitional stages, but skeletons with broken vertebral columns are very rare; the Serranidae are all straight (Fig. 16).

The state of preservation is very good: over 95% of the specimens are complete, and their skull bones, vertebral columns, scales, and fin rays are articulated. Isolated heads or tails (except in one specimen) are absent.

Very good preservation of scales *in situ* of most of the fish (except for the Argentinidae) is characteristic of this assemblage. The state of preservation of scales of the Argentinidae proved indecipherable because of diagenetic alteration.

Most specimens have bones articulated, and close to their anatomical position; only 4% of specimens have skull bones that are slightly displaced. Many specimens have jaws gaped (Fig. 9 — beds WAP 1 and WAP 2).

All specimens have their complete abdominal part. All specimens, except two, have all complete fins. Pectoral fins tend to have rays close to each other, and close either to the body or directed to the ventral side (see Fig. 10A). Often one fin has rays close one to another while a second fin has rays in a
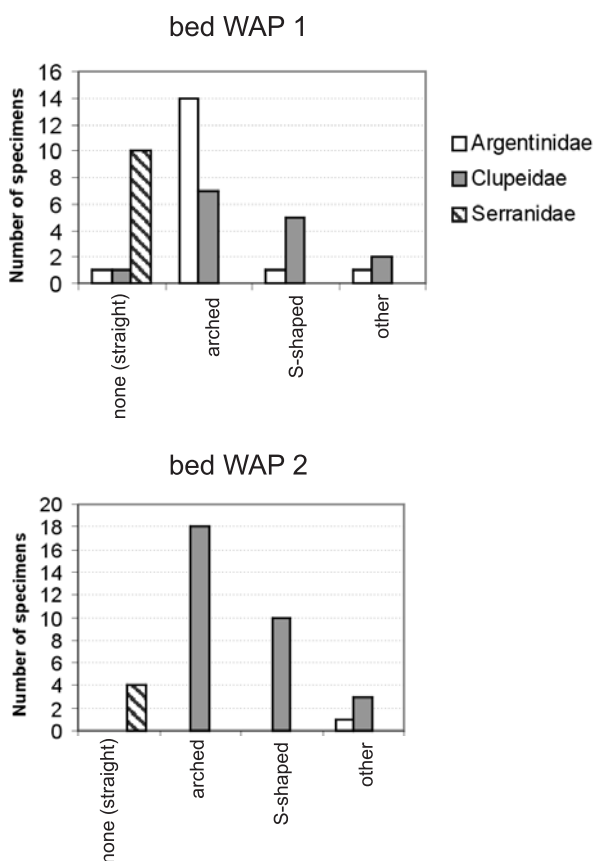
bed WAP 1

bed WAP 2

Fig. 11. Types of skeleton curvature in Assemblage A in beds WAP 1 and WAP 2

fan-like arrangement — set flabellate (Fig. 10C). Occasionally both fins have their rays flabellate (Fig 10B). Pelvic fins tend to be reclined close to the body. In some instances, as for, pectoral fins, one fin has rays close to each other, and the second fin has rays flabellate. Usually, pectoral and pelvic fins of a given specimen have the same setting. Dorsal fins have rays usually close one to another and reclined close to the dorsal body outline (Fig. 10D), or rays are set obliquely to the dorsal body outline (Fig. 10E). Anal fins have variable settings; they often have either rays close to each other and reclined close to the ventral body outline, or rays are set obliquely to the ventral body outline, or rays are disordered (Fig. 10F). Caudal fins usually have their rays close to each other.

Assemblage A occurs the in the laminated variety of the Tylawa Limestones. Apart from fish skeletons, only a single piece of fossil wood has been found. The quantity of separate bones and scales is very small. Rare coprolites contain bones and scales.

ASSEMBLAGE B

Specimens of 5 species of the families: Clupeidae, Argentinidae, Paralepididae, Gadidae, and Serranidae occur in this assemblage. Sizes of bodies are diverse: Clupeidae 7.5–10 cm, Argentinidae 3.5–5 cm, Paralepididae 20–30 cm, Gadidae 5–31 cm, Serranidae 2–7 cm.

Usually, the fish lie either on the left or on the right side of the body, but sometimes only a part of the body lies on its side, the rest being either dorso-ventrally flattened, or placed obliquely to the symmetry plane. Some bodies lie with their symmetry plane at an oblique angle to the bedding plane.

The skeletons are variably deformed. As in Assemblage A, some deformations are characteristic for the given families as follows (Fig. 12): the Argentinidae tend to be slightly arched; the rare Clupeidae are all twisted into an S-shape; the Gadidae are slightly arched (76% of specimens) or straight (Fig. 17); the Paralepididae are straight; the Serranidae are mostly straight (86% of specimens; Fig. 17), the rest being slightly arched.

The state of preservation is very diverse and ranges from very good (complete skeletons) to very bad (disarticulated and dispersed bones). About 50% of the skeletons have signs of disarticulation, but the body parts are often preserved in spatial proximity. Sometimes it is possible to ascertain that a small concentration of isolated scales and bones is the rest of the body of one fish. The remains recognised (small concentrations) are bones and scales of the Gadidae and the Serranidae, the most abundant families in the assemblage.

About 50% of specimens have lost some scales. Scales have detached uniformly from all over the body or from a small part of the body. Many specimens are devoid of scales in the front or caudal part of their body, but in other parts of the body they have well-preserved scales. Specimens without scales are very rare. For dominant families (the Gadidae and the Serranidae) diagrams have been made (Fig. 13), which show frequencies of specimens with all scales *in situ* and with detached scales. Those diagrams show that there was a variable pattern of detachment of scales in the Gadidae and the
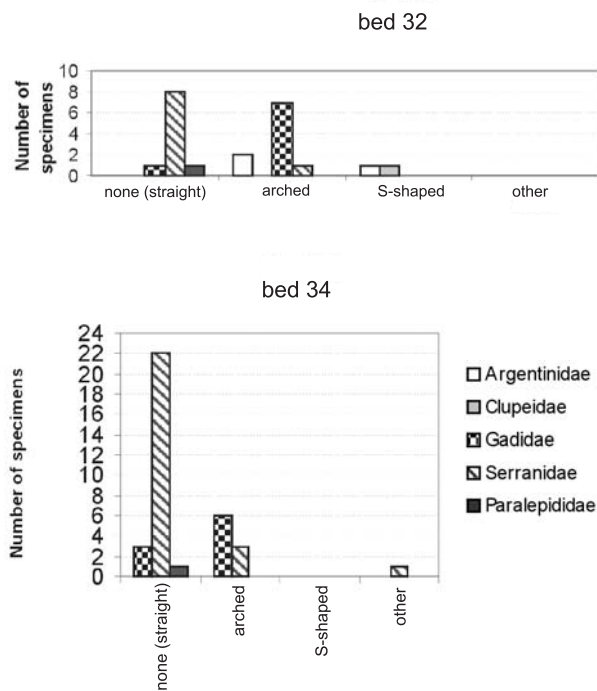
bed 32

bed 34

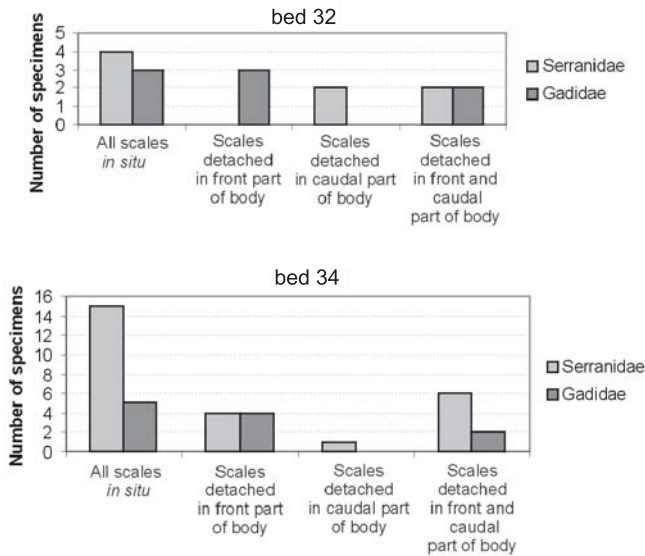Fig. 12. Types of skeleton curvature in Assemblage B in beds 32 and 34

Fig. 13. Preservation of scales in the Gadidae and the Serranidae in beds 32 and 34 (Assemblage B)

Serranidae. The Gadidae have scales detached from the front part of the body or uniformly all over the body. The caudal part of the gadid body is usually well preserved (Fig. 14); the boundary between the skin with scales and without scales is usually distinct. There are no specimens of the Gadidae with scales detached only from the caudal part of their body. The Serranidae have scales detached usually from the front part of their body or uniformly from all over the body. Some specimens of the Serranidae with scales detached only from the caudal part of their body are present; those specimens have the caudal fin and back parts of their dorsal and anal fins decomposed.

Many specimens have a disarticulated skull. In the collection of the Argentinidae, the Serranidae, and the Gadidae from bed 32, as many as 41% of the specimens have a disarticulated skull. In the collection of Gadidae and Serranidae from bed 34, nearly 60% of the specimens have a disarticulated skull.

Gadidae usually have a badly preserved skull. Bones usually rest in spatial proximity to the rest of the skeleton (Figs. 18 and 19). Many specimens have jaws gaped (Fig. 9 — beds 32 and 34).

Gadidae often have vertebral columns in a few pieces or nearly complete but with a few vertebrae not articulated. Displacement of vertebrae usually appears in the abdominal part. About 40% of specimens have their abdominal skin torn. Many specimens have incomplete fins. Pectoral and pelvic fins tend to have rays close to each other (Fig. 10A). Those fins often have rays disintegrated, but close to the rest of the skeleton. Dorsal and anal fins usually have rays set obliquely to the body outline (Fig. 10E) or rays close to each other and reclined close to the body outline (Fig. 10D); rarely rays are disordered. The disordered setting occurs usually when all skeletons have signs of decomposition. The Serranidae often have spines of dorsal and anal fins set obliquely to the body outline, but soft rays are reclined close to the body outline. Caudal fins usually have their rays close to each other. Very rarely they are decomposed.

The disintegration processes of the fishes have undergone various pathways. In the front part of the body (especially in the Gadidae) these processes usually were more intense than in the caudal part. In some cases, the abdominal part is decomposed but the skull is complete. In some instances, the skull is disintegrated but the abdominal part is well preserved. Where a skull is disintegrated, the abdominal part is usually also poorly preserved. Fins display a variable setting, not dependent upon the state of preservation of the other parts of the skeleton. Assemblage B occurs in laminated claystones with peloids. Apart from fish skeletons, only one piece of an alga was found. The quantity of separate bones and scales is quite large. Rare coprolites contain bones and scales. Three specimens display a unique preservation, having remains of other fish in the abdominal part of their skeletons. In two cases the complete skeleton of a small fish is preserved inside the abdominal cavity of a bigger fish (Fig. 20). These small fishes have their fins reclined close to their body outline, the vertebral column parallel to that of the bigger fish, and the heads di-
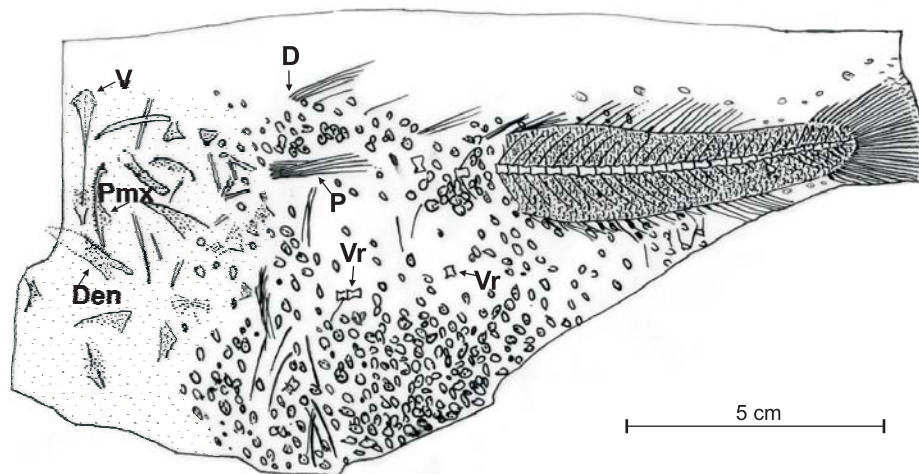

Fig. 14. A gadid skeleton (RU 03.9.1.) partially disintegrated in front part of the body, caudal part with scales (scales in proximity to the rest of skeleton), spotted area — concentration of skull bones; Den — dentale, Pmx — praemaxillare, V — vomer, P — pectoral fin, Vr — vertebrae, D — dorsal fin (arrow shows its beginning, and the end of head); from claystones below WAP 2
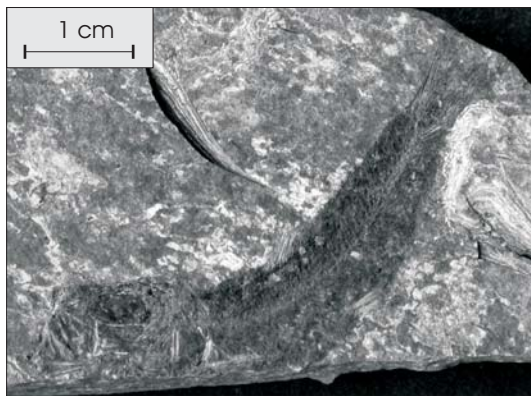
Fig. 15. A clupeid skeleton (RU 03, WAP 1.29.) arched, from bed WAP 1(Assemblage A)

Fig. 16. A serranid skeleton (RU 03, WAP 1.43.), abdominal cavity and orbit space are black, from bed WAP 1 (Assemblage A)
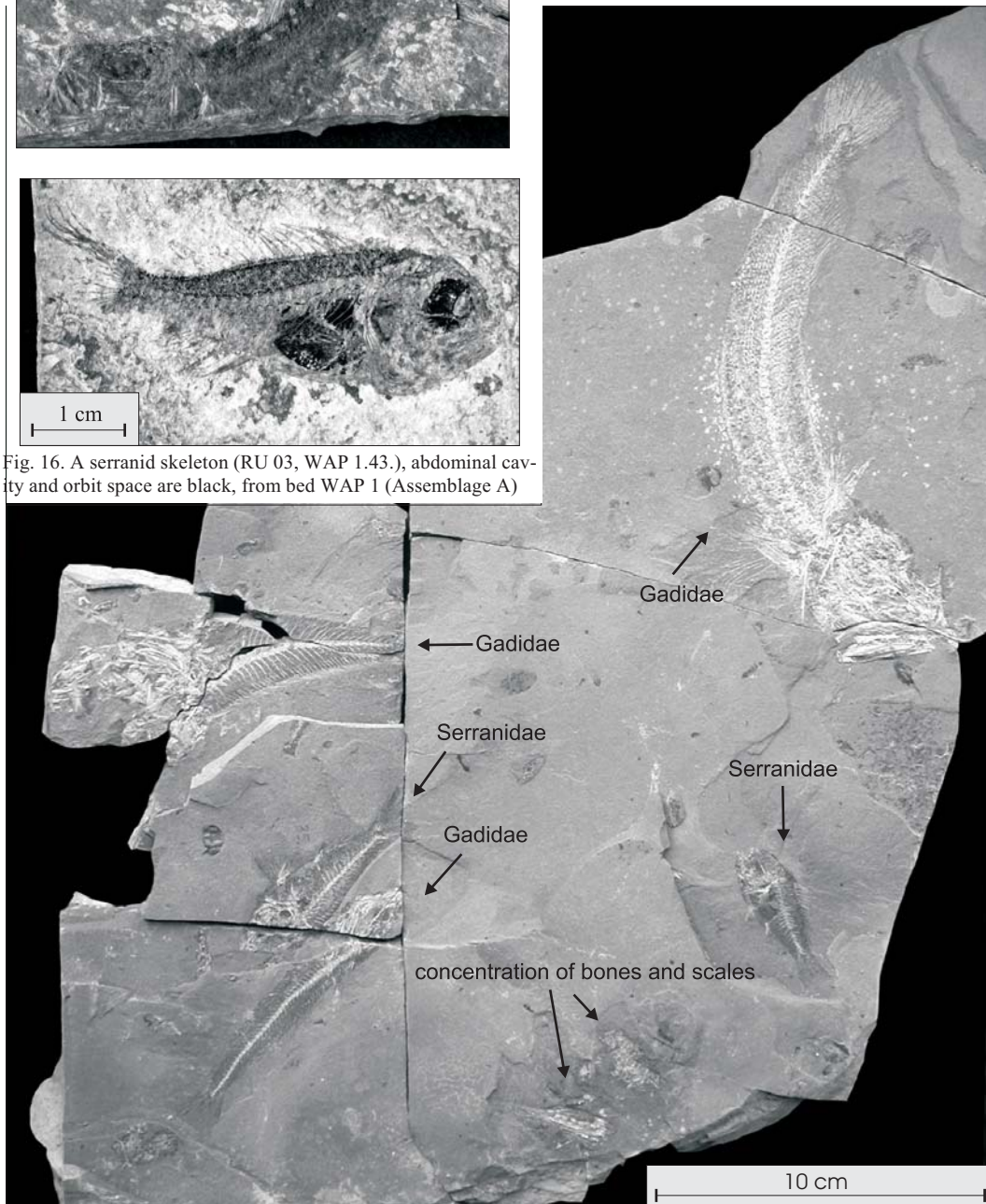
Fig. 17. Part of bed 34, to show packing and setting of skeletons (Assemblage B)

rected to the tail of the bigger fish, all features indicative of a swallowed prey. Such swallowed remains are typical of the skeletons of *Holosteus mariae* (Menner, 1948), the species whose occurrence in the Outer Carpathians in Poland, and its taphonomy is the subject of a separate publication. One of the swallowed fish is a representative of the Serranidae, the second is of the Argentinidae.

DISCUSSION

Complete and partially disarticulated skeletons occur exclusively in horizontally laminated rocks. This observation is in agreement with those of Jerzmańska and Kotlarczyk (1968), and Wilson (1988*a*).

Fig. 18. A serranid skeleton (RU 03.34.33.) with signs of disintegration in front and caudal parts of the body;
bed 34 (Assemblage B)

Fig. 19. A gadid skeleton (RU 03.34.10.) with signs of disintegration in front part of the body;
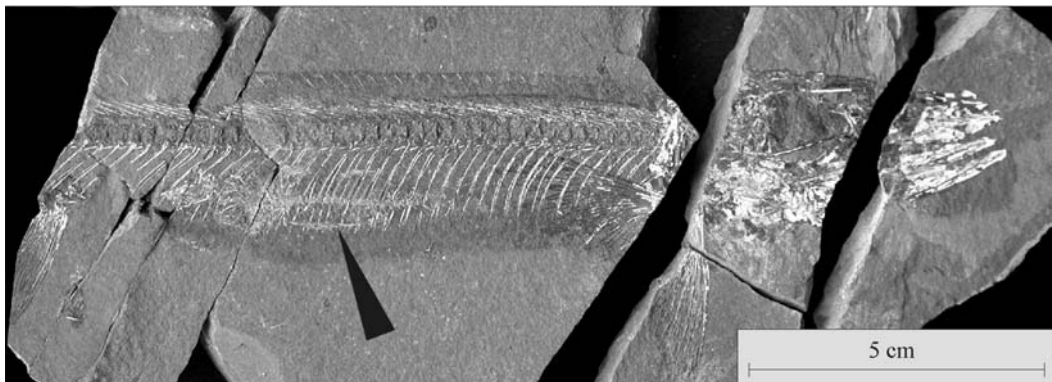caudal part well preserved with scales; bed 34 (Assemblage B)

Fig. 20. A paralepidid skeleton (RU 01.32.23.) — *Holosteus mariae* (Menner, 1948) with a serranid skeleton
in its abdominal cavity (arrowed); bed 32 (Assemblage B)

Very good preservation of fish skeletons in the Tylawa Limestones, and especially the *in situ* presence of scales in the Clupeidae, indicate an early cessation of decay after fish death (Weiler, 1929).

The state of preservation of skeletons in claystones indicates that carcasses arrived at the sea floor in various stages of decay of the soft tissue; the time during which the carcasses remained at the sea floor was variable. Small concentrations of bones and scales are probably either remains of carcasses in which the soft tissues have decomposed partially during transport of carcasses from the place of death to that of their burial (Schäfer, 1972), or alternatively they may be regurgigated gastric residues (pellets) (Wilson, 1987). The presence of detached scales and bones in proximity to the rest of the skeleton indicates that partially disarticulated skeletons have arrived at the sea floor as complete bodies soon after fish death and that all processes of decomposition (detaching of scales and bones) occurred at the place of burial. Most of the detached scales and bones are usually close to the skull and abdominal part of the fish, which is characteristic of the decay process in any fish (Schäfer, 1972; Wilson and Barton, 1996). Disintegration patterns are similar to those resulting from a process of decay caused by microorganisms, but the influence of the scavengers and other factors can not be excluded. Fins have variable settings, not dependent upon the preservation state of other parts of the skeleton. The preservation in Assemblage B confirms the data of Schäfer (1972) that processes of decay may have a variable pattern in the same environmental conditions. The process of decay is usually most intense in the abdominal cavity and in the head, but the detailed pattern of the detaching of scales and the disintegration of other parts of the skeleton may vary between representatives of different families, and within the same family. The Gadidae tend to show a displacement of vertebrae more often than the other families. The displacement of vertebrae could be caused either by the pressure of decay gases in the abdominal cavity, by a disarticulation of vertebrae as a consequence of decay of soft tissue, or by mechanical deformation when a carcass has reached the sea floor (Schäfer, 1972). The presence of the coprolites indicates that there were predators present in the basin. One of the predators, *Holosteus mariae* (Menner, 1948), was recognised by the exceptional preservation of gut contents. However, determining the nature of other predators seems to be impossible for the material studied (Wilson, 1987).

Deformation of axial skeletons in the described material is similar to patterns recognised in other localities in the Carpathians and elsewhere (Weiler, 1929; Hecker and Merklin, 1946; Jerzmańska, 1960). It is thought that S-shaped and arched curvatures are caused by natural post-mortem contraction of muscles (Jerzmańska, 1960). According to Hecker and Merklin (1946), the arched curvature is natural post-mortem bending, but the S-shaped pattern results from the pressure of weak bottom currents on an arched skeleton. It is thought that irregular deformations of the axial skeleton are caused by action of local bottom currents (Hecker and Merklin, 1946; Jerzmańska, 1960). Strong deformations may be caused, ac-

cording to Hecker and Merklin (1946), when soft tissue is partially decomposed. Breakage of the axial skeleton could be a natural consequence of post-mortem bending (Weiler, 1929); it could be also an effect of the carcass impacting the sea floor (Schäfer, 1972). Preservation patterns in the material described agree with the observations of Jerzmańska (1960), that a lack of deformation is observed mostly in representatives of fishes with a high body. Some types of deformation are specific for representatives of particular families (Figs. 11 and 12): the Clupeidae tend to be arched or twisted into an S-shape. Their bending varies from slight to strong. Such types of deformation in this family were noted by Weiler (1929), Hecker and Merklin (1946), Horbach (1956), Jerzmańska (1960) and are also recognisable in illustrations of some other reports (Daniltshenko, 1960 pl. 18, fig. 1; pl. 19; pl. 21, fig. 1; Ciobanu, 1977 pl. 7–12, 14, figs. 1 and 2). The Argentinidae tend to be slightly arched, the Gadidae are usually straight or slightly arched (Daniltshenko, 1960 pl. 3, figs. 1 and 2, pl. 6–7), the Paralepididae are straight, and the Serranidae tend to straight (Daniltshenko, 1960 pl. 25, figs. 2–4).

Skeletons from Rudawka Rymanowska are predominantly straight, arched and twisted into an S-shape. Other types of deformations are rare. There are no signs of the action of bottom currents, and some types of deformation are specific for representatives of particular families, indicating that arched and S-shaped curvatures can be presumed to be natural post-mortem bending. There are many skeletons with their jaws gaped, but the frequency of skeletons with jaws closed/gaped varies in each bed (Fig. 9), suggesting that the cause of death was not the same for all specimens. The gaped jaws indicate sudden death of the fish caused by either asphyxiation, poisoning, heat shock or choking up of the gills by suspended particles (Ciobanu, 1977; Elder and Smith, 1988; Wilson, 1988*b*).

Most of the taphonomic features in the material from Rudawka Rymanowska are known from other assemblages of Oligocene ichthyofauna in the Outer Carpathians and the Caucasus. There are some common features, such as the deformation of the axial skeleton, the varied patterns of disintegration of skeletons, the presence of complete skeletons with jaws closed or gaped, and the absence of directional orientations of the skeletons (Hecker and Merklin, 1946; Horbach, 1956; Jerzmańska, 1960, 1968; Jerzmańska and Kotlarczyk, 1968, 1975; Ciobanu, 1977). The biostratonomic observations made in other localities have given contradictory results, for instance concerning poisoned bottom waters or the life conditions of benthic biota (Hecker and Merklin, 1946; Kotlarczyk and Jerzmańska, 1988).

The state of preservation of fishes in the Tylawa Limestones is much better than in the stratigraphically younger Jasło Limestones from Sobniów. Most of the fish from Sobniów do not have scales, except for the Clupeidae, unlike those in the Tylawa Limestones at Rudawka Rymanowska which all have well-preserved scales. There are many skeletons which are strongly curved (into a circle or loop) in deposits of the Caucasus (see Hecker and Merklin, 1946), but not deformations such as occur at Rudawka Rymanowska. There are no isolated heads

and tails in the exposures studied, whereas such specimens are noted from the Jasło Limestones at Sobniów (Jerzmańska, 1960), and the Maikop shales in the Black River of the Caucasus (Hecker and Merklin, 1946).

CONCLUSIONS

The presence and state of preservation of fish remains in the section studied depends on the lithology. Sandstones and shales, displaying features of low-density turbidity-current deposits, contain isolated fish bones and scales segregated as detrital elements. Fish skeletons in the laminated Tylawa Limestones (taphonomic Assemblage A) are considered to be pelagic in origin; those in the laminated claystones (taphonomic Assemblage B) are probably also pelagic.

The taphonomic assemblages studied differ from each other mainly in the state of preservation of the skeletons: Assemblage A contains very well preserved skeletons; Assemblage B contains only 40 to 60% of well preserved skeletons, the rest being partially disintegrated.

The very good state of preservation skeletons in the Tylawa Limestones indicates an early cessation of decay after death.

In the claystones, the fish carcasses arrived at the sea floor in various stages of decay of soft tissue and the duration of resting of the carcasses on the sea floor was variable. Disintegration patterns are similar to those resulting from decay caused by microorganisms.

Deformations of vertebral columns in all studied specimens are considered to be natural post-mortem features.

This approach to the fish taphonomy, in the facies-controlled section at Rudawka Rymanowska, may prove useful for the recognition of physical conditions on the Oligocene sea floor in other parts of the Carpathians (Slovakia, Romania) and coeval basins of the Caucasus. A further step may be to decipher not only the burial, but also the life conditions of fish entombed in the various Oligocene sequences of the Carpathians and the Caucasus.

REFERENCES

BIEŃKOWSKA M. (2002) — Tafonomia ichtiofauny i środowisko sedymentacji osadów oligoceńskich w Rudawce Rymanowskiej koło Krosna. Unpub. M. Sc. Thesis; Faculty of Geology, Univ. Warsaw.

BÖHM B. (1930) — Stratygrafia trzeciorzędu karpackiego na podstawie fauny rybiej. Pamiętnik Pierwszego Zjazdu Geologiczno-Naftowego we Lwowie, 14–15 grudnia 1929, Warszawa-Borysław-Lwów: 67–79.

BOUMA A. H. (1962) — Sedimentology of some flysch deposits. Elsevier, Amsterdam/New York.

CIOBANU M. (1977) — Fauna fosilă din oligocenul de la Piatra Neamt (The fossil fauna of the Piatra Neamt). Editura Academiei Republicii Socjaliste Romănia, Bucuresti.

DANILTSHENKO P. G. (1960) — Kostistye ryby maikopskikh otlozheniy Kavkaza. Trudy Paleont. Instit., **77**.

DAVIS J. C. (1986) — Statistics and data analysis in geology, 2nd ed. Wiley. New York.

ELDER R. L. and SMITH G. R. (1988) — Fish taphonomy and environmental inference in paleolimnology. Palaeogeogr., Palaeoclim., Palaeoecol., **62**: 577–592.

FOLK R. L. (1959) — Practical petrographic classification of limestones, Am. Ass. Petrol. Bull., **43**: 1–38.

HACZEWSKI G. (1989) — Coccolith limestone horizons in the Menilite-Krosno series (Oligocene, Carpathians) — identification, correlation and origin (in Polish with English summary). Ann. Soc. Geol. Pol., **59** (3–4): 435–523.

HECKER R. F. and MERKLIN R. L. (1946) — Ob osobennostakh zahoronenya ryb w maikopskikh glinastykh slancakh sewernoy Osietii. Izvest. Akad. Nauk SSSR, Otdelenya Biologitshnykh Nauk, **6**: 647–674.

HORBACH L. P. (1956) — Ichtiofauna i uslovlya obrazovanya otlotsheny menilitovoy serii Karpat, Avtoreferat. Lvovskiy Gosydarstvenny Universitet im. Iv. Franko, Lvov.

JERZMAŃSKA A. (1960) — Ichthyofauna from the Jasło shales at Sobniów (in Polish with English summary). Acta Palaeont. Pol., **5** (4): 367–412.

JERZMAŃSKA A. (1967) — Argentinidés (poissons) fossiles de la série ménilitique des Karpathes. Acta Palaeont. Pol., **12** (2): 195–209.

JERZMAŃSKA A. (1968) — Ichthyofaune des couches f́ ménilite (flysch des Karpathes). Acta Palaeont. Pol., **13** (3): 379–481.

JERZMAŃSKA A. and KOTLARCZYK J. (1968) — Ichtyofaunal assemblages in the Menilite Beds of the Carpathians as indicators of sedimentary environment (in Polish with English summary). Ann. Soc. Geol. Pol., **37** (1): 39–61.

JERZMAŃSKA A. and KOTLARCZYK J. (1975) — Fossils of the Quassi-Sargasso assemblage in the Menilite beds of the Skole unit, Polish Carpathian Mountains (in Polish with English summary). Kwart. Geol., **19** (4): 875–886.

JERZMAŃSKA A. and KOTLARCZYK J. (1976) — The beginnings of the Sargasso assemblage in the Tethys?. Palaeogeogr., Palaeoclim., Palaeoecol., **20**: 227–306.

JERZMAŃSKA A. and KOTLARCZYK J. (1991) — Zasięgi pionowe bytowania ichtiofauny znalezionej w serii menilitowo-krośnieńskiej Karpat Rzeszowskich. Materiały XIV Konferencji Paleontologów w Karpatach Rzeszowskich "Paleontologia a batymetria", Kamionka k. Rzeszowa 1991: 22–24.

JUCHA S. (1969) — Łupki jasielskie, ich znaczenie dla stratygrafii i sedymentologii serii menilitowo-krośnieńskiej (Karpaty fliszowe). Prace Geol. Pol. Akad. Nauk, **52**.

KIDWELL S. M., FÜRSICH F. T. and AIGNER T. (1986) — Conceptual framework for analysis and classification of fossil concentrations. Palaios, **1**: 228–238.

KOTLARCZYK J. and JERZMAŃSKA A. (1976) — Biostratigraphy of Menilite Beds of Skole Unit the Polish Flysch Carpathians. Bull. Acad. Pol. Sc. Sér. Sc. Terr., **24** (1): 55–62.

KOTLARCZYK J. and JERZMAŃSKA A. (1988) — Ichtiofauna w stratygrafii Karpat. Prz. Geol., **36** (6): 346–351.

MASTELLA L. and KONON A. (2002) — Tectonic bending of the Outer Carpathians in the light of joints analysis in the Silesian Nappe (in Polish with English summary). Prz. Geol., **50** (6): 541–550.

MENNER W. W. (1948) — Ichtiofauna maikopskikh otlozheniy Kavkaza. Trudy Instit. Geol Nauk, vyp. 98, **30**: 51–62.

PICARD M. D. (1971) — Classification of fine-grained sedimentary rocks. J. Sediment. Petrol., **41**: 179–195.

PICKERING K., STOW D., WATSON M. and HISCOTT R. (1986) — Deep-water facies, processes and models: a review and classification scheme for modern and ancient sediments. Earth-Science Rev., **23**: 75–174.

RYCHLICKI J. (1909) — Przyczynek do fauny ryb karpackich łupków menilitowych. Kosmos, **34** (7/9): 749–764.

SCHÄFER W. (1972) — Ecology and palaeoecology of marine enviroments. Univ. Chicago Press, Chicago.

STOW D. A. V. and PIPER D. J. W. (1984) — Fine-grained sediments: deep water processes and facies. Geol. Soc. Blackwell Sc. Pub., Oxford, U.K.: 611–646.

SZYMCZYK W. (1978) — Clupeid scales from the Menilite Beds (Palaeogene) of the Carpathians. Acta Palaeont. Pol., **23** (3): 387–403.

ŚWIDNICKI J. (1986) — Oligocene Zeiformes (Teleostei) from the Polish Carpathians. Acta Palaeont. Pol., **31** (1–2): 111–135.

ŚWIDNICKI J. (1988) — Juveniles of some Oligocene Antigonia (Caproidae, Teleostei) from the Polish Carpathians. Acta Palaeont. Pol., **33** (3): 249–257.

WEILER W. (1929) — Über das Vorkommen isolierter Köpfe bei fossilen Clupeiden. Senckenbergiana, **11**: 40–43.

WILSON M. V. H. and BARTON D. G. (1996) — Seven centuries of taphonomic variation in Eocene freshwater fishes preserved in varves: paleoenvironments and temporal averaging. Paleobiology, **22** (4): 535–542.

WILSON M. V. H. (1987) — Predation as a source of fish fossils in Eocene Lake Sediments. Palaios, **2**: 497–504.

WILSON M. V. H. (1988a) — Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. Palaeogeogr., Palaeoclimat., Palaeoecol., **62**: 609–623.

WILSON M. V. H. (1988b) — Taphonomic processes: information loss and information gain. Paleoscene 9. Geosc. Canada, **15** (2): 131–148.