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Taphonomy of Oligocene teleost fishes from the Outer Carpathians of Poland

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ABSTRACT:

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The Oligocene ichthyotaphocoenoses from the Outer Carpathians of Poland are dominated by skeletons of actinopterygian (only teleost) fishes. Their taphonomy was studied in six localities of the Menilite-Krosno Series (Błażowa, Jamna Dolna 1, Jamna Dolna 2, Rudawka Rymanowska, Wola Czudecka, Wujskie). Over 1700 specimens of variably complete fish skeletons, representative of 20 actinopterygian families, were studied.

The taphonomic analysis of the skeletal disarticulation and its pattern, deformations of the vertebral column (curved, broken), arrangement of jaws and fins, the spatial array of skeletons with regard to the embedding sediment, as well as identification of unusually preserved specimens, indicate that all of the ichthyotaphocoenoses have resulted from a long-term accumulation of fish carcasses at the burial place, at a very low sedimentation rate, under anoxic conditions in, and above, the sediment/water interface. Two assemblages from the Tylawa Limestone Horizon have acquired their unusually good preservation state due to the penetration of calcium carbonate into soft tissues of corpses at the burial place. In other deposits (shales, marls) the fish skeletons are more or less disarticulated as a result of decay in a calm environment. Each of the ichthyotaphocoenoses displays some features indicative of mass mortality events (e.g. high density of individuals, the presence of individuals with jaws agape, high number of juveniles); none of them has a set of features indicating it unequivocally. The cause and/or conditions of death were not the same for all individuals. Only some individuals died instantaneously during mass mortalities, whereas the majority died over a period of time as a result of senility, diseases, or other circumstances. All of the ichthyotaphocoenoses show features typical of both necro- and thanatocoenoses. The associated flora and fauna, e.g., amphipods, land-derived dragonflies and bird feathers, indicate that the taphocoenoses originated as a result of accumulation of biotic remains from various environments. Fishes and associated remains settled on the bottom successively, and thus their assemblages display features typical of necrocoenoses. Evidence of fish predation is reported for the first time from the Menilite-Krosno Series of Poland.

Key words: Taphonomy; Teleost fishes; Ichthyotaphocoenoses; Fish predation; Menilite-Krosno Series; Oligocene; Outer Carpathians; Poland.

INTRODUCTION

Six well-documented localities provide a unique opportunity to investigate teleost fish taphonomy in the Oligocene deposits of the Outer (Flysch) Carpathians in Poland. Although fish remains or complete skeletons have long been reported from the successions studied and from other age-equivalent strata of the Carpathian

Chain, their taphonomy is still poorly known. Most of the taphocoenoses in these deposits are dominated by teleosts, and they will be referred to herein as **ichthyotaphocoenoses**. Apart from the bony fishes, the studied deposits yielded macroflora: algae and terrestrial plants (Świdziński 1948; Kadyi 1958; Jerzmańska 1960; Jucha and Kotlarczyk 1961; Jucha 1969; Dżułyński and Sanders 1962; Dżułyński 1963, 2001; Jerzmańska and Kotlarczyk 1975, 1976; Brzyski 1979; Zastawniak and Worobiec 1997; Rajchel and Uchman 1998; Jerzmańska *et al.* 2001; Bieńkowska 2002, 2004b); marine macrofauna, rarely recorded: large foraminifers, corals, bivalves, gastropods, scaphopods, bryozoans (Bieda, De Cizancourt, Grzybowski, Kropaczek, Książkiewicz, Pazdro, Rogala, Świdziński, Wiśniowski, Wójcik – *fide* Jucha and Kotlarczyk 1961, Jucha and Krach 1962, Koszarski and Żytko 1961), nautiloids (Świdnicka 2007), crabs (Jerzmańska 1967b; Jerzmańska and Kotlarczyk 1968; Kotlarczyk 1991), lobsters (Glaessner 1965), amphipods (Jerzmańska *et al.* 2001; pers. comm. K. Jażdżewski 2006), isopods (Van Straelen 1928; Kotlarczyk 1979), sea urchins (Ślączka 1963), cartilaginous fishes (Dżułyński and Sanders 1962; Dżułyński 1963; Jerzmańska and Jucha 1963; Jerzmańska and Kotlarczyk 1988; Dżułyński 2001; Kotlarczyk *et al.* 2006; Bieńkowska-Wasiluk and Radwański 2009) and turtles (Kadyi 1958; Młynarski 1959); as well as terrestrial macrofauna: one dragonfly (Jerzmańska *et al.* 2001) and diverse remains of birds (Bocheński and Szymczyk 1979; Bocheński 1996; Bocheński and Bocheński 2008).

The aim of this study is to: (i) determine bottom conditions under which the fish carcasses were entombed, and recognize whether or not these carcasses were affected by scavengers or bottom currents; (ii) determine the character of the ichthyotaphocoenoses (necro- or thanatocoenoses, in terms as used by Davitašvili 1945 and Radwańska 2007).

The studied fishes, collected by the present author (930 specimens, housed at the Faculty of Geology, University of Warsaw) in five localities (Błażowa, Jamna Dolna 2, Rudawka Rymanowska, Wola Czudecka, Wujskie), were supplemented by 780 specimens from the locality Jamna Dolna 1, from Prof. A. Jerzmańska's collection (c/o Department of Palaeozoology, Institute of Zoology, University of Wrocław, Institutional abbreviation ZPALWr.).

This paper presents the main ideas of my PhD thesis (see Bieńkowska 2007b) prepared under the supervision of Prof. Andrzej Radwański at the Faculty of Geology, University of Warsaw. Some results of the study were published previously (Bieńkowska 2006, 2007a, 2008a, b; Bieńkowska and Wasiluk 2008).

HISTORY OF FISH RESEARCH

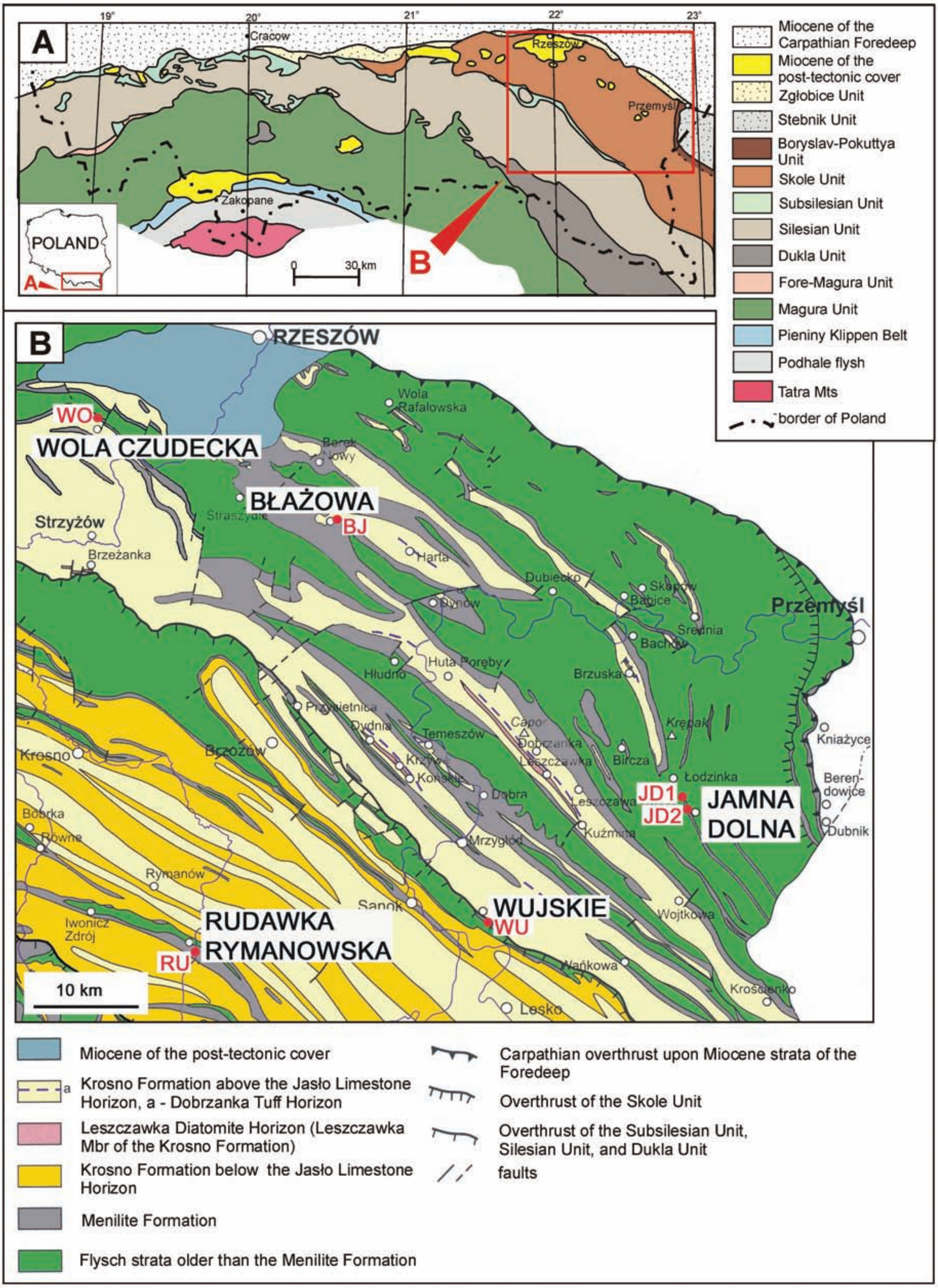
The teleost fishes from the Outer Carpathians of Poland have been studied since the mid-19th Century (Heckel 1850; Gorjanović-Kramberger 1879, 1882; Rychlicki 1909; Bośniacki 1911; Paucă 1931; Jerzmańska 1958, 1960, 1967a, 1968, 1974, 1979, 1985; Jerzmańska and Jucha 1963; Jerzmańska and Kotlarczyk 1968, 1975, 1976; Jerzmańska and Świdnicka 2003; Śmigielska 1962; Szymczyk 1978, 1979; Świdnicki 1986, 1988a, 1988b, 1990; Tyler and Gregorová 1991; Tyler *et al.* 1993; Jerzmańska *et al.* 2001; Żabrowski 2002; Gregorová 2004; Kotlarczyk *et al.* 2006), and these were mostly taxonomic studies. The first taphonomic data were published by Jerzmańska (1960, pp. 407–409) in her primarily taxonomic report on the ichthyofauna from the Jasło Limestone Horizon (formerly the Jasło Shales). Some further taphonomic observations, accompanying the discussions about the origin of the fish-bearing deposits, were provided by Jerzmańska and Kotlarczyk (1973, pp. 545–546; 1975, p. 880) and Kotlarczyk *et al.* (2006 pp. 25, 37–41). Taphonomic analyses of fishes from the Tylawa Limestone Horizon were published by the author (Bieńkowska 2002, 2004a, b).

LOCALITY DETAILS

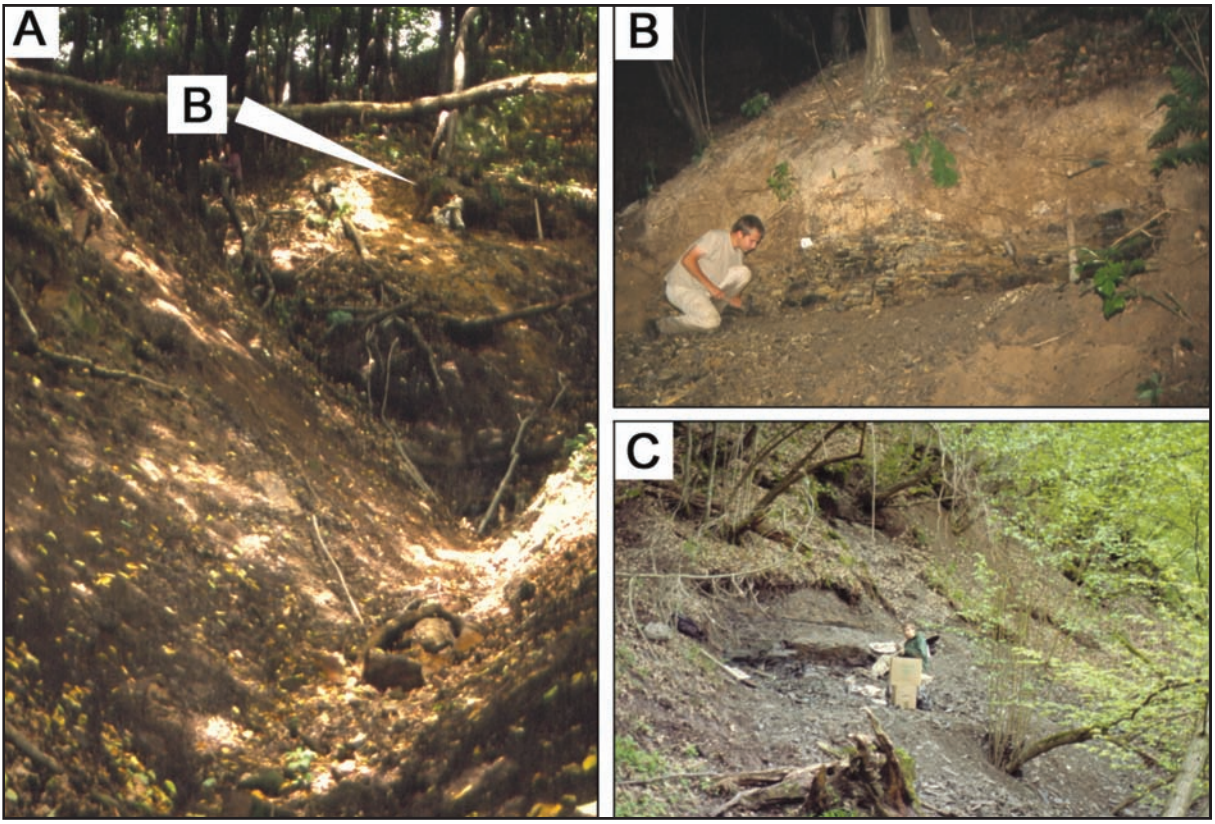
The localities studied represent three tectonic units of the Outer (Flysch) Carpathians: the Skole, Subsilesian, and the Silesian units (see Text-fig. 1A, B). The stratigraphy of the fish-bearing successions is documented by calcareous nannoplankton and is dated as Oligocene (see Kotlarczyk *et al.* 2006, p. 10, fig. 2). Lithostratigraphically, they are a part of the Menilite-Krosno Series, and belong to the Menilite and the Krosno formations (Text-fig. 3), described in detail by Kotlarczyk *et al.* (2006).

Błażowa (BJ): this locality lies in in the Skole Unit, 20 kilometres south of Rzeszów (Text-fig. 1B). The fossils were excavated in a ravine (see Text-fig. 2A, B) in the southern slope of the Wielka Góra hill (Trzy Krzyże), about 1 km east of a small bridge over the Piątkówka stream. Exposure B_4 of Kotlarczyk *et al.* (2006) is also located in this ravine.

The succession (Text-fig. 4) is composed of black shales of platy- and leaf-like fissility, grey and black laminated shales, grey nonfissile shales and fine-grained sandstones. Most of the shales of leaf-like fissility contain at their base a silt or sand lamina, or a slightly lenticular sandstone. The black shales of platy fissility and the



Text-fig. 1. Location maps: **A** – Tectonic units of the Outer Carpathians of Poland to show the setting of the area with fish-bearing localities (after Książkiewicz 1962, Żytko *et al*. 1989, modified), **B** – Location of fish-bearing sectins (geological map after Jucha 1969 and Kotlarczyk *et al*. 2006): Błażowa (BJ), Jamna Dolna 1 (JD1), Jamna Dolna 2 (JD2), Rudawka Rymanowska (RU), Wola Czudecka (WO), and Wujskie (WU)



Text-fig. 2. General view of fish-bearing exposures. **A** – Błażowa ravine, during the fieldwork in July 2003; the arrow shows the excavation for fishes, **B** – Close-up view of the excavation, **C** – Jamna Dolna 2, during field work in May 2004

grey and black laminated shales contain fish skeletons. One of the layers of the grey shale is slightly bioturbated. The black shales of platy fissility display a parallel lamination in thin sections, as is shown by colour variability (Text-fig. 6A). Skeletons excavated in layers 9, 7, 5, and 4 form ichthyotaphocoenoses BJ.9, BJ.7, BJ.5 and BJ.4 respectively.

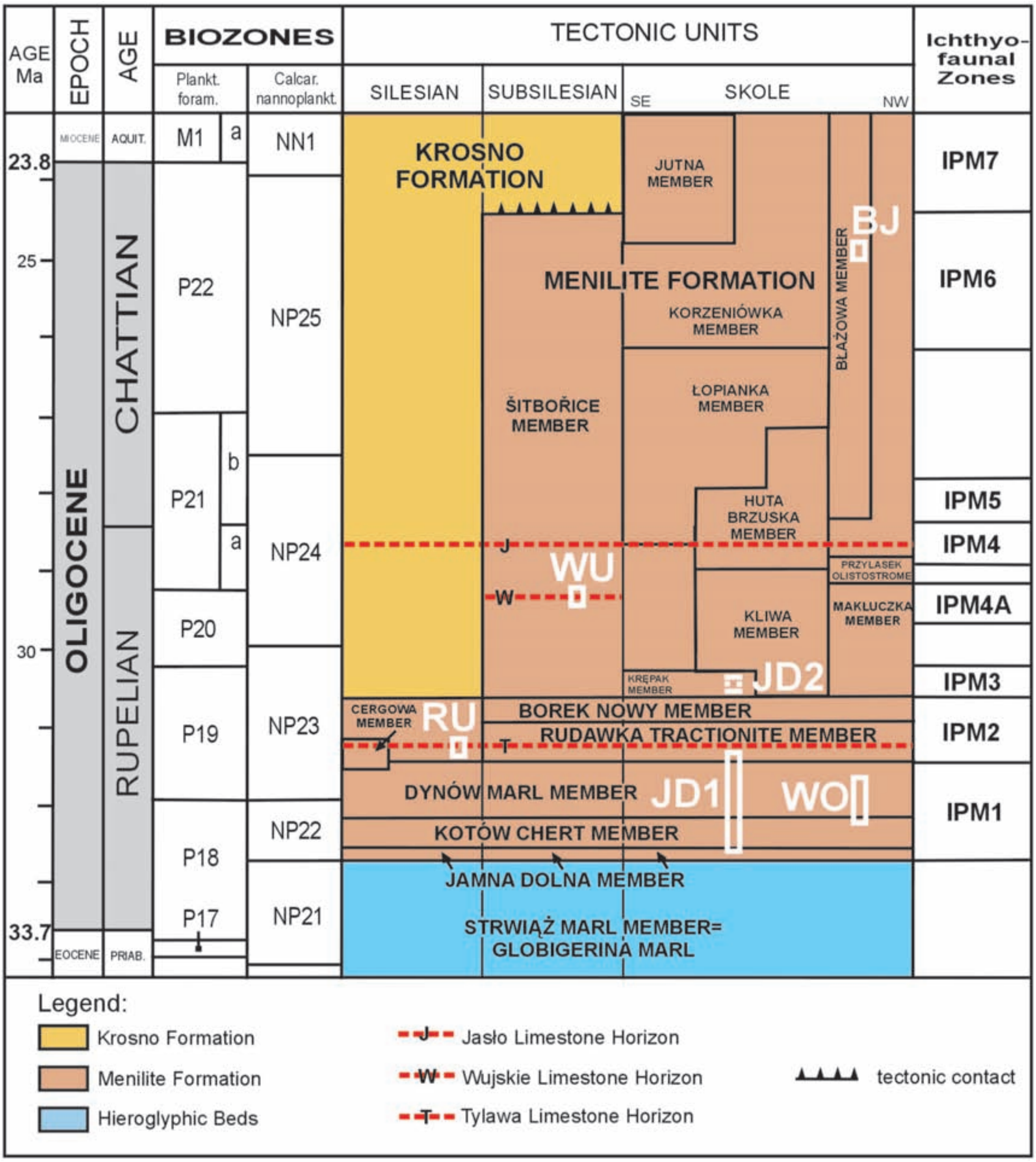
The Błażowa (BJ) section lies in the middle part of the Błażowa Member. The presence of *Argyropelecus* sp. indicates the ichthyofaunal zone IPM6 (*Argyropelecus cosmovicii*), recognized formerly in exposure B_4 (Kotlarczyk *et al.* 2006, p. 66, table 26). These are the youngest deposits dealt with in this study.

Jamna Dolna 1 (JD1): this locality has been known since 1953 (Jerzmańska 1968; Jerzmańska and Kotlarczyk 1968; J_{AC} and J_{DG} in Kotlarczyk et *al.* 2006). It is situated in the Skole Unit, 20 km south-west of Przemyśl (Text-fig. 1B), in the area of the former village of Jamna Dolna, c. 8 km southeast of Bircza. The specimens studied were collected between 1963 and 1966 by Professors A. Jerzmańska, J. Kotlarczyk and their collaborators, about 1 km south of a bridge over the river Wiar at Trójca, in the upper part of the escarpment of the Jamninka river (right tributary of the river Wiar), in an exposure approximately 70 m long and 15 m high (Jerzmańska and Kotlarczyk 1968). Between 2003 and 2006, a few specimens were collected by the present author; nowadays the exposure is covered by scree to half of its height.

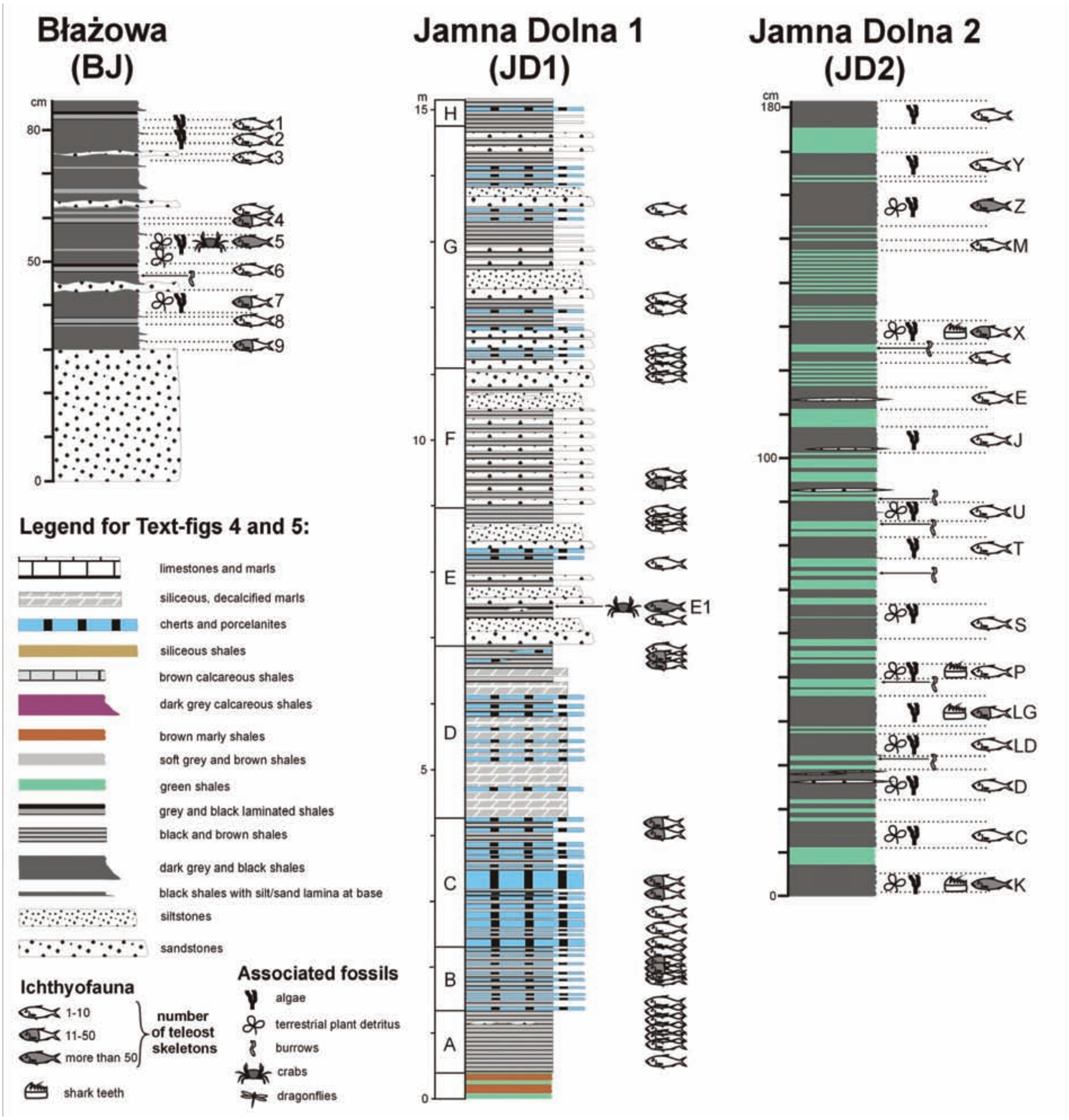
The 15-m thick fish-bearing section (Text-fig. 4) is composed of nine lithological units (recognised by Jerzmańska and Kotlarczyk 1968), briefly characterized below. Unit **A** consists of black and brown shales of platy and leaf-like fissility. Unit **B** includes brown shales, light-brown porcelanites (rocks silicified less than cherts), and cherts; the shales are either laminated, displaying platy fissility, or non-laminated of sheet-like fissility. Unit **C** contains mainly dark brown cherts and light brown to white porcelanites. Unit **D** includes mainly light, soft shales that have been thought to be decalcified marls (Jerzmańska and Kotlarczyk 1968). Unit **E** consists of intervals in which medium-bedded sandstones grade up into lenticular, cross-laminated sand laminae in laminated mudstones, and farther upwards into black and brown shales. A 1-cm thick layer of laminated brown shales, termed E1, is distinguished by the abundance of fishes. In thin section these shales display parallel lamination (Text-fig. 7C, D). Unit **F** contains intervals of thin-bedded, cross-laminated sandstones, which grade up into brown mud shales, and farther upwards into clay shales. Unit **G** includes cherts, porcelanites, brown laminated and non-laminated shales, and sandstones. Unit **H** contains mainly brown shales and cherts.

The fish skeletons occur in brown shales: non-laminated and of sheet-like fissility (units B, D), non-laminated and of platy fissility (units B, C, D), laminated (units C, D, layer E1), laminated by silt and cherts (unit E), and laminated by cherts (units B and C). The skeletons excavated in units B, C, D, E and layer E1 form ichthyotaphocoenoses JD1.B, JD1.C, JD1.D, JD1.E and JD1.E1 respectively. Fish skeletons yielded by layer E1 are excluded from ichthyotaphocoenose JD1.E because of the presence of the species *Trachinus minutus* (Jonet, 1958), which does not occur here in other units (see Jerzmańska and Kotlarczyk 1968, Kotlarczyk *et al*. 2006).

The Jamna Dolna 1 (JD1) section represents the oldest part of the succession studied. The base of the section (lithological units A and B, see Text-fig. 4) is included in the Jamna Dolna Member. The overlying



Text-fig. 3. Stratigraphic position of the fish-bearing sections: Błażowa (**BJ**), Jamna Dolna 1 (**JD1**), Jamna Dolna 2 (**JD2**), Rudawka Rymanowska (**RU**), Wola Czudecka (**WO**), and Wujskie (**WU**), in relation to the litho- bio-, eco-, and chronostratigraphy schemes of Oligocene deposits of the Outer Carpathians of Poland (the scheme compiled by Prof. Kotlarczyk, see Kotlarczyk *et al*. 2006; p. 10, fig. 2 and p. 96, fig. 33) shales and marls are included in the Kotów Chert Member (lithological unit C) and the Dynów Marl Member (lithological unit D) respectively. The Dynów Marl Member correlates with nannoplankton biozone NP23 (Krhovský 1981). It has been suggested (see Kotlarczyk *et al.* 2006) that the upper boundary of the Dynów Marl Member has a position slightly lower than formerly indicated, and should be placed just above the marls (the upper, shaly part of unit D should be included in the Rudawka Tractionite Member). The upper part of the section represents the Rudawka Tractionite Member. Units A–C represent the ichthyofaunal zone IPM1 (*Scopeloides glarisianus* and *Eomyctophum limicola*), and units D–G the ichthyofaunal zone IPM2 (*Glossanodon musceli* and *Palaeogadus simonescui*); both zones were recognized by Kotlarczyk *et al*. (2006, p. 66, tab. 26). Units B and C are assigned to ichthyofaunal subzone IPM1-C.$_{\mathrm{SUB}}$. The latter characterises the first mass-occurrence of the genus *Centriscus* in the Oligocene and is referred to as the *1st Centriscus* Event (Kotlarczyk *et al*. 2006). The layer E1 records the mass-occurrence of the genus *Trachinus* and is referred to by Kotlarczyk *et al*. (2006) as the *Trachinus* Event and ichthyofaunal subzone IPM2-T.$_{\mathrm{SUB}}$.

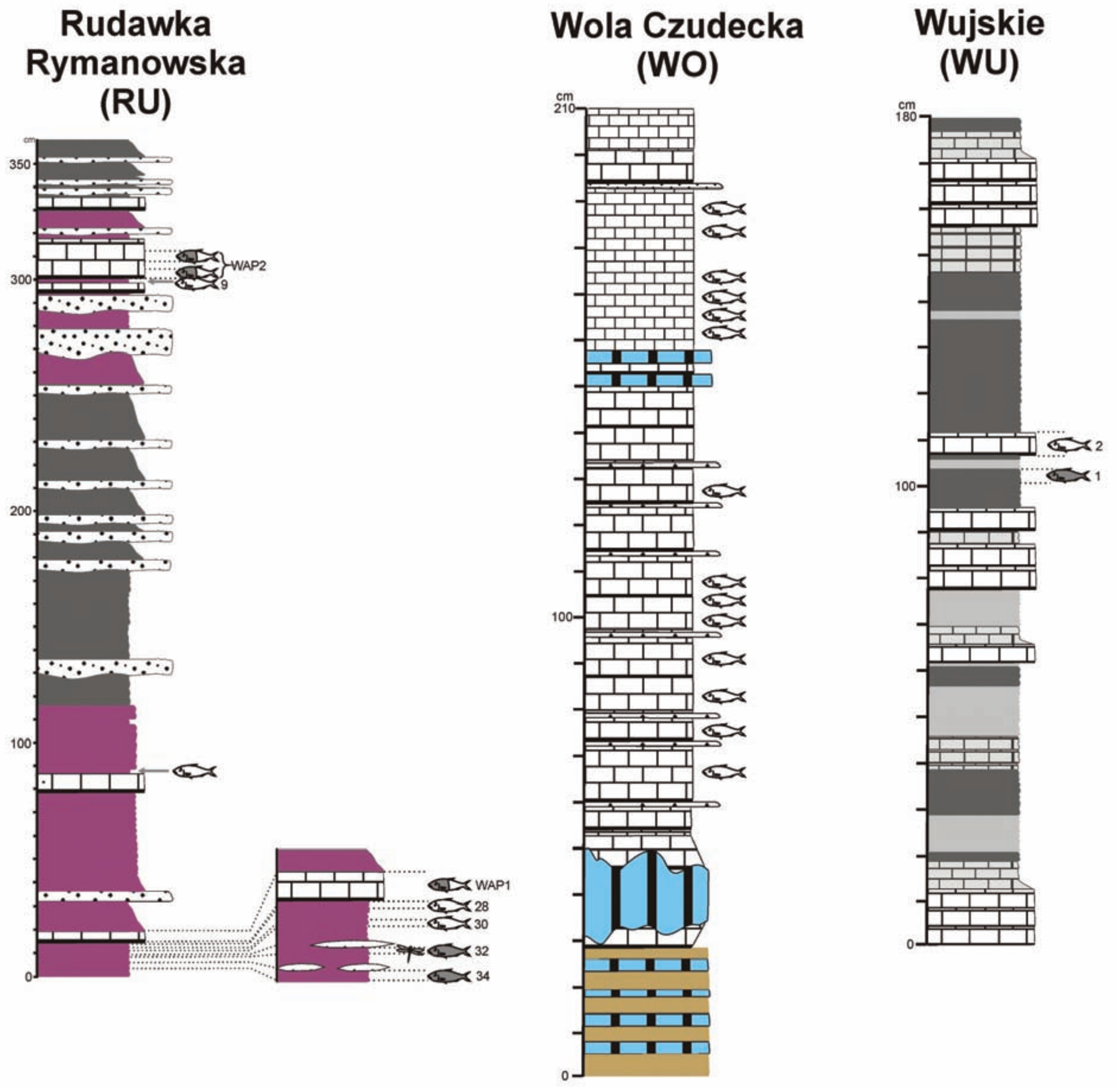


Text-fig. 4. Fish-bearing sections: Błażowa (**BJ**), Jamna Dolna 1 (**JD1**), and Jamna Dolna 2 (**JD2**), to show the fossil-bearing layers

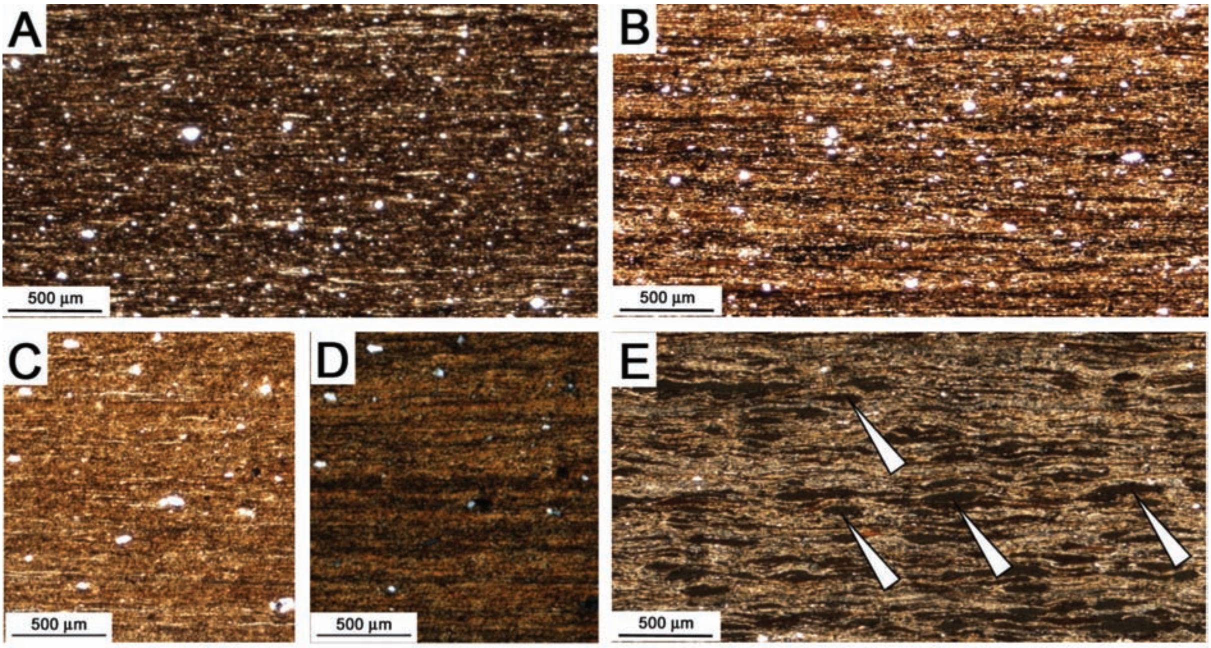
Jamna Dolna 2 (JD2): this locality is situated c. 2 kilometres south of Jamna Dolna 1 (Text-fig. 1B). It consists of a few exposures on the eastern side of the Jamninka River. The fossils come from an artificial exposure widening the natural outcrop of shales in the slope just above the flood plain, about 50 m from the river bed. The exposure was about 2 m high and about 5 m wide (Text-fig. 2C).

The fish-bearing section (Text-fig. 4), 180 cm thick, includes an abundance of black shales of platy, and leaf-like fissility, intercalated with green shales and sandstones. Most of the black shales of platy fissility contain fish skeletons and oblate concretions (less than 1 cm in diameter) of pyrite. Many layers display slightly pronounced parallel lamination. As seen in thin sections of laminated shales from the layer T and non-laminated shales of platy fissility in layers K, LG, X and Z (see Text-fig. 4), parallel lamination (Text-fig. 6B) is present. The fish-bearing layers K, LG, X and Z consist of black shales of platy fissility interbedded with black shales of leaf-like fissility without fishes. The latter can contain a silt/sand lamina at the base, or may be underlain by a thin layer of sandstone. The sandstones occur as thin beds or lenses; four of the green shale layers contain minute burrows.

Skeletons excavated in layers K, LG, X and Z form ichthyotaphocoenoses JD2.K, JD2.LG, JD2.X and JD2.Z respectively.



Text-fig. 5. Sections: Rudawka Rymanowska (**RU**), Wola Czudecka (**WO**), Wujskie (**WU**) to show the fossil-bearing layers; explanations as for Text-fig. 4

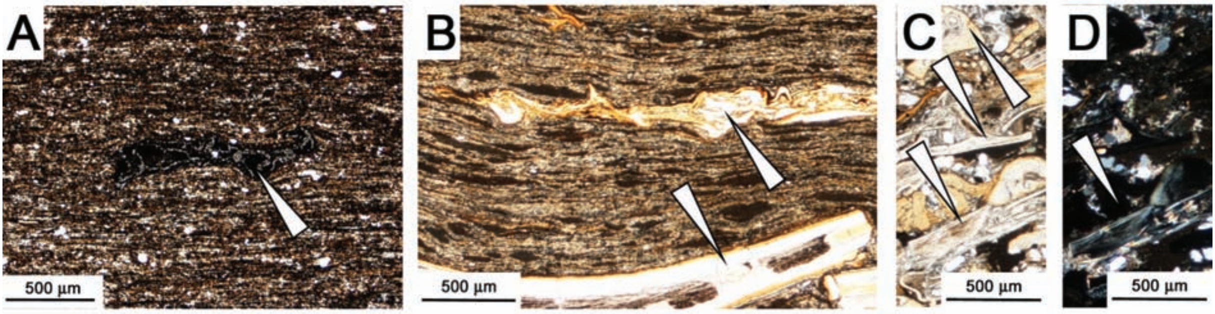


Text-fig. 6. Parallel lamination of shales, thin sections: **A** – Black shale from Błażowa (layer 5), II nicols; **B** – Black shale from Jamna Dolna 2 (layer X), II nicols; **C-D** – Brown shale from Jamna Dolna 1 (layer E1), C – II nicols, D – X nicols; **E** – Dark-grey calcareous shale from Rudawka Rymanowska (layer 32; calcareous peloids arrowed), II nicols

The Jamna Dolna 2 (JD2) section most probably starts about 15 m above the top of the Dynów Marl Member. The association of green and black shales resembles those of the Krępak Member. The taxonomic composition of the fish assemblage suggests ichthyofaunal zone IPM3, albeit the index species have not been found.

Rudawka Rymanowska (RU): this locality is situated in the southern part of the Silesian Unit, some 60 kilometres south of Rzeszów (Text-fig. 1B). Exposures are available in the river bed of the Wisłok and in its tributary stream, near the village of Rudawka Rymanowska. The fossils were collected between 1998 and 2001 (Bieńkowska 2002, 2004a,b), as well as subsequently in 2003 and 2005, in the exposures RU 01, RU 02 and RU 03 (see Bieńkowska 2004b, fig. 1).

The fish-bearing section (Text-fig. 5), 350 cm thick, appearing in these three exposures, includes shales, limestones and sandstones. Dark grey calcareous and non-calcareous shales are interbedded with fine-grained sandstones. Some of the shales of leaf-like fissility contain fish scales and bones, and mica flakes. These shales and the sandstone-shale couplets show normal grading. Some of the dark grey calcareous shales of platy fissility, with indistinct lamination, contain fish skeletons. Lamination and peloids are distinct in thin sections of these shales. Laminated and non-laminated limestones (layers WAP1 and WAP2, see Text-fig. 5), known as the Tylawa Limestones, consist of the first (oldest) and second layer of the four included in the Tylawa Limestone Horizon. The fish skeletons are contained in laminated limestones.



Text-fig. 7. Fish bones (arrows) as seen in thin sections. **A** – Black shale from Błażowa (layer 5), II nicols; **B** – Dark-grey calcareous shale from Rudawka Rymanowska (layer 32), II nicols; **C-D** – Fine-grained calcareous sandstone from Rudawka Rymanowska, C – II nicols, D – X nicols

Skeletons excavated in layers 34, 32, WAP1 and WAP2 form ichthyotaphocoenoses RU.34, RU.32, RU.WAP1 and RU.WAP2 respectively.

The Rudawka Rymanowska (RU) section represents the Tylawa Limestones, which constitute a separate key horizon (marker bed). The ichthyofauna is characteristic of ichthyofaunal zone IPM2 (*Glossanodon musceli* and *Palaeogadus simonescui*).

Wola Czudecka (WO): The locality is situated in the Skole Unit, some 20 kms southwest of Rzeszów (Text-fig. 1B). The fossils were collected in a small quarry, about 1 km northwest of the village of Wola Czudecka. The part of the quarry where the fishes were excavated is inaccessible nowadays.

The fish-bearing section (Text-fig. 5), 15 m thick, consists of marls called the Dynów Marls, interbedded with rare limestones, cherts and sandstones. In some of the marl layers the arrangement of detrital plant remains or fish scales indicates normal grading. The marl unit is underlain by a unit of cherts and siliceous shales. Fish skeletons occur in the laminae separating the beds of marls or limestones.

All skeletons excavated from the unit of marls form ichthyotaphocoenose WO.

The marls of Wola Czudecka (WO) belong to the Dynów Marl Member, which is correlated with nannoplankton biozone NP23 (Krhovský 1981) and ichthyofaunal zone IPM1 (*Scopeloides glarisianus* and *Eomyctophum limicola*). The cherts and shales at the base of the section are included in the Kotów Chert Member.

Wujskie (WU): The locality is situated in the Subsilesian Unit, some 45 kms southwest of Przemyśl (Text-fig. 1B). The fossils were collected along the slope on the left bank of an unnamed tributary of the Wujski stream, near the church at Wujskie. This exposure was distinguished as WZ_6 by Kotlarczyk *et al.* (2006).

The fish-bearing section (Text-fig. 5), 180 cm thick, consists of non-calcareous black, green, and grey shales, calcareous brown shales, and a small portion of laminated and non-laminated marls and limestones. These limestones and marls are classified as the Wujskie Limestones (Kotlarczyk *et al*. 2006). The shales of platy and leaf-like fissility can contain mica flakes and fish scales. Fish skeletons occur either in a single layer of black shales of platy fissility, or in a single layer of limestones.

The fish skeletons were excavated from layer 1 of the black shales (ichthyotaphocoenose WU.1), an equivalent of 'layer 42' of Kotlarczyk *et al*. (2006) from the Przysietnica locality.

The Wujskie (WU) section embraces limestones of the Wujskie Limestone Horizon (Kotlarczyk *et al*. 2006). The ichthyofauna studied by Kotlarczyk *et al*. (2006) records the local ichthyofaunal subzone IPM4A (*Carpathospinosus propheticus* and *Centriscus* sp.), which is recognized solely in the Subsilesian Unit. This subzone records the second Oligocene mass-occurrence of the genus *Centriscus*, distinguished as the *2nd Centriscus* Event by Kotlarczyk *et al*. (2006).

TAPHONOMY OF THE FISHES

The degree of disarticulation of fish skeletons studied herein is highly variable. In this study, the term *fish skeleton* is used for articulated skeletons and also for disarticulated skeletons which, in extreme cases, are represented by only a few bones of a single individual.

The taphonomic analysis investigated (1) the degree of skeleton disarticulation; (2) the state of preservation of disarticulated skeletons; (3) the spatial arrangement of fish skeletons in the rock matrix; (4) the state of preservation of the vertebral column (e.g. straight, curved, broken), as well as of fins and jaws; (5) unusual cases of preservation; and (6) diagenesis of skeletal elements.

In the sections studied, isolated skeletal elements are common in sandstones, shales and marls. Within particular layers, there is a gradual upward size decrease in skeletal elements, indicating their redeposition. The bones are always much larger than the associated mineral grains (Text-fig. 7C, D). The scales tend to occur together with mica flakes, and both are oriented horizontally in shales.

Skeletal elements occur in coprolites or probably gastric ejecta, which are quite common in the ichthyotaphocoenoses.

The isolated scales and bones are usually almost *in situ*, having been detached from the carcass and displaced. Alternatively, they have been derived from the carcasses of fishes which decayed far from the burial place and then were transported to burial place. Skeletal elements are oriented horizontally (Text-fig. 7A, B).

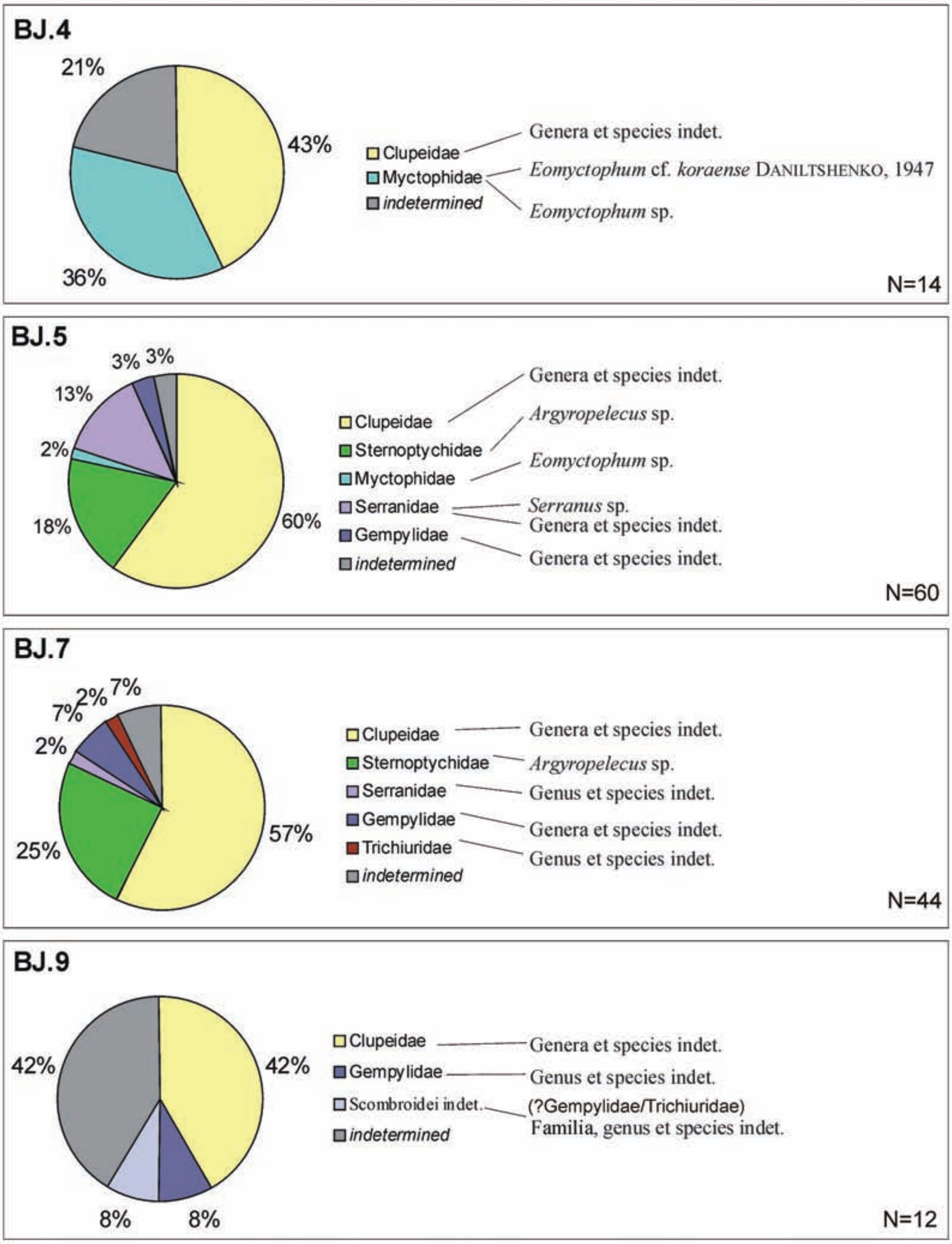
In some layers, the fish skeletons are so abundant that they are visible on each slab (e.g. layer E1 at Jamna Dolna 1, Text-figs 4 and 38; layer K at Jamna Dolna 2, Text-figs 4 and 39; and layer 1 at Wujskie, Text-figs 5 and 37B).

Of 930 fish skeletons collected by the present author, some 150 specimens were complete. The rest were devoid of some parts due to natural or accidental breaks in the rocks. The incompleteness of such specimens did not exclude them from taphonomic analysis if the required key feature was preserved; this means that different numbers of specimens were used for each particular analysis.

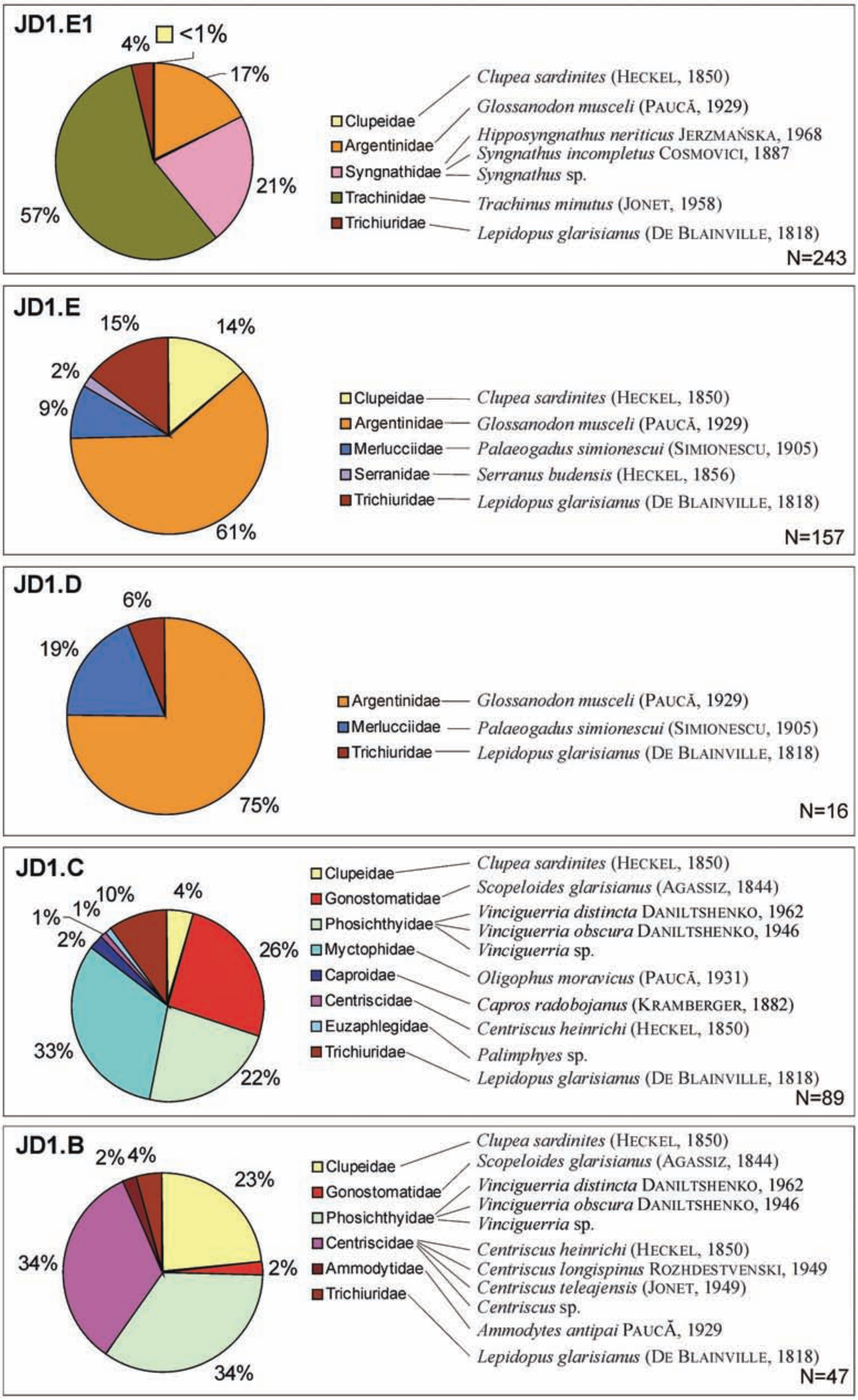
For illustration of the taphonomic features (Text-figs 14–40), the photos are presented in pairs: in natural view; and with an outline of the fish drawn around the fringe of skeletal elements, either articulated or arranged close to their anatomical position.

Taxonomy

The ichthyofauna from Jamna Dolna 1, described by Jerzmańska (1968) and Jerzmańska and Kotlarczyk (1968), was identified by A. Jerzmańska. The ichthyofauna from the remaining five localities was identified by the present author. The taxonomic assignment of some of the specimens studied needs explanation. The species *Glossanodon musceli* (Paucă, 1929), was previously assigned to the family Argentinidae (Jerzmańska 1968, Jerzmańska and Kotlarczyk 1968, Kotlarczyk *et al*. 2006). Recently, Prokofiev (2005a, p. 14) assigned some specimens of this species to a separate genus, *Austromallotus*



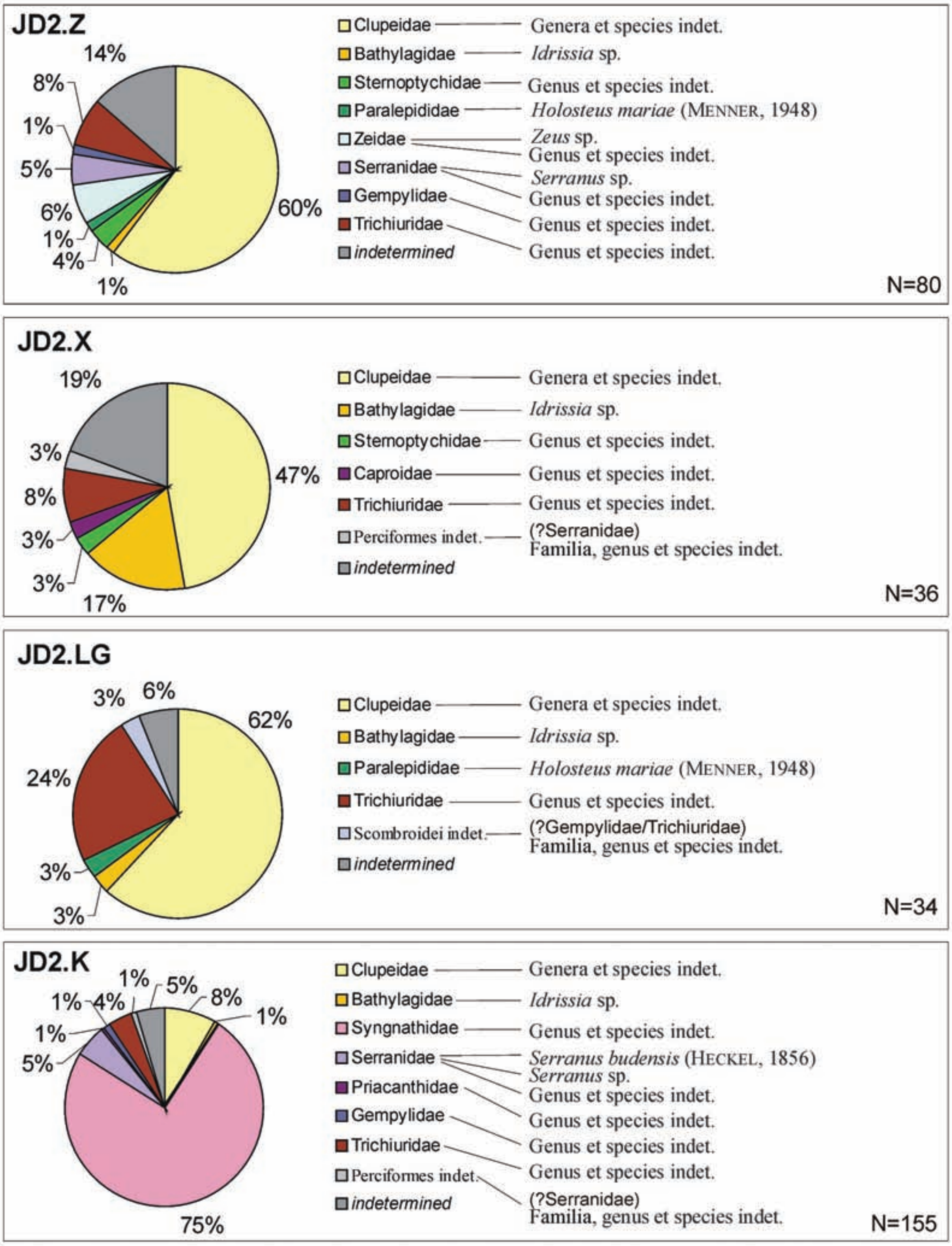
Text-fig. 8. Taxonomic composition of ichthyotaphocoenoses BJ.4, BJ.5, BJ.7, BJ.9 from the locality Błażowa; N – number of specimens examined



Text-fig. 9. Taxonomic composition of ichthyotaphocoenoses JD1.E1, JD1.E, JD1.D, JD1.C, JD1.B from the locality Jamna Dolna 1; N – number of specimens examined

Prokofiev, 2005, classified in the family Osmeridae. Because a full revision of the specimens previously assigned to *G. musceli* has not yet been undertaken, Jerzmańska's (1968) interpretation of this species is followed herein. Specimens from the locality Jamna Dolna 1, assigned by A. Jerzmańska (1968) to *Eomyctophum limicola* Daniltshenko, 1960, are referred herein to *Oligophus moravicus* (Paucă, 1931), following Gregorová (2004), who studied specimens from this locality. The specimens assigned to *Vinciguerria obscura* Daniltshenko, 1946, and *Vinciguerria distincta* Daniltshenko, 1962, remain as assigned by A. Jerzmańska (1968), albeit Prokofiev (2002) suggested their inclusion in the new genus *Eovinciguerria* Prokofiev, 2002.

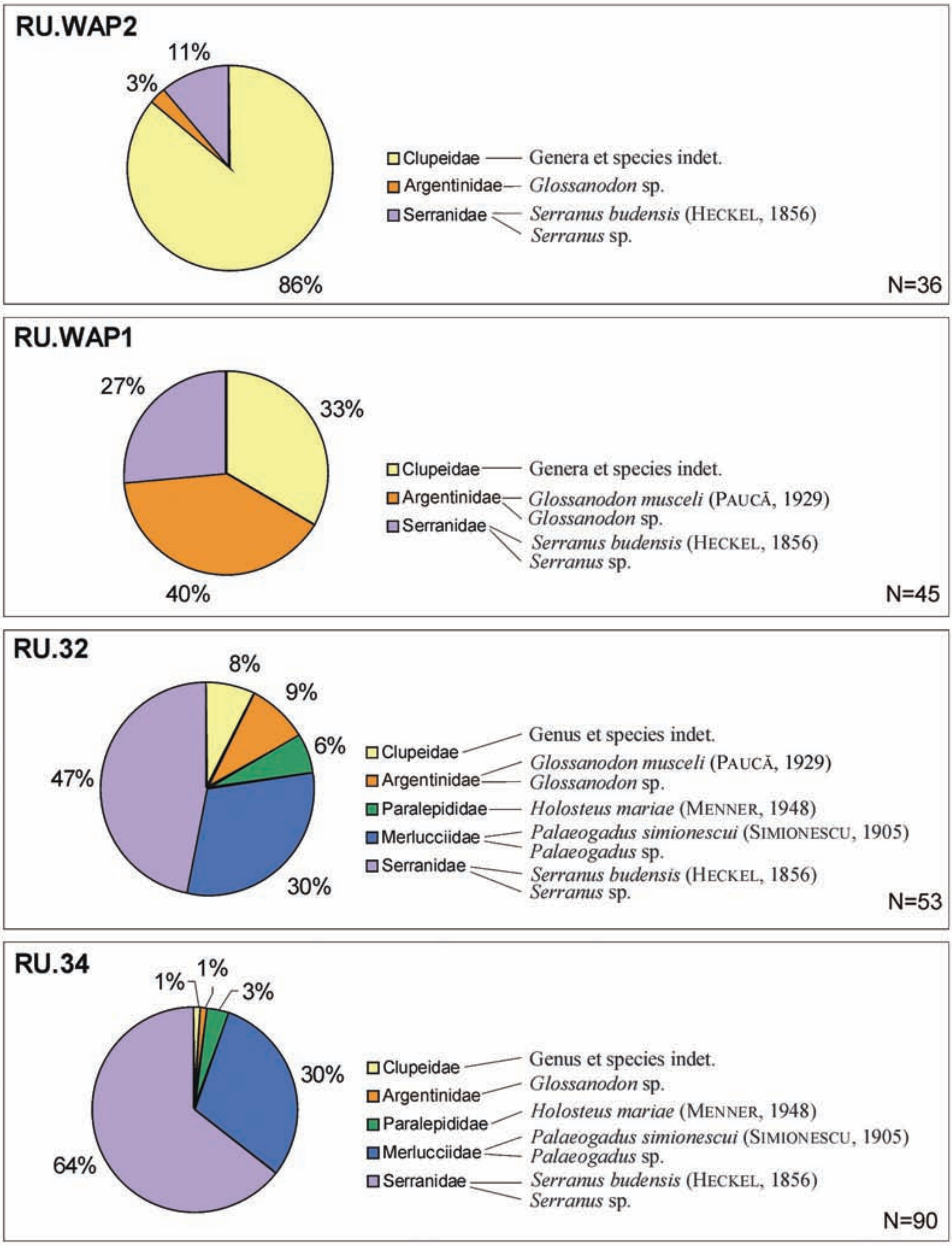
The taxonomic composition of all the ichthyotaphocoenoses studied is highly variable (Text-figs 8–13).



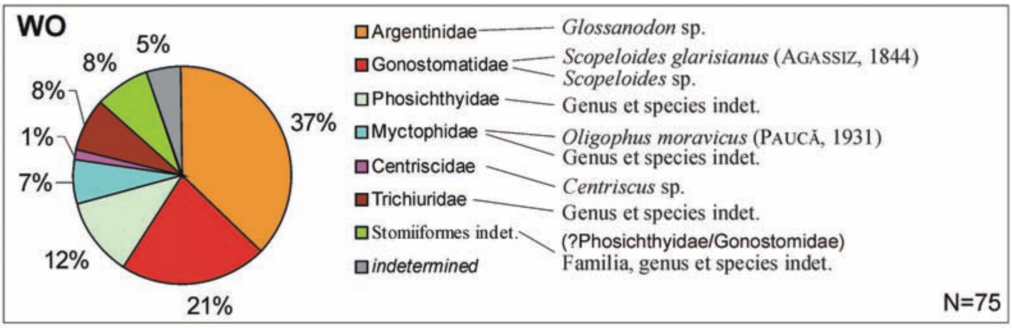
Text-fig. 10. Taxonomic composition of ichthyotaphocoenoses JD2.Z, JD2.X, JD2.LG, JD2.K from locality Jamna Dolna 2; N – number of specimens examined

Diagenesis of skeletal elements

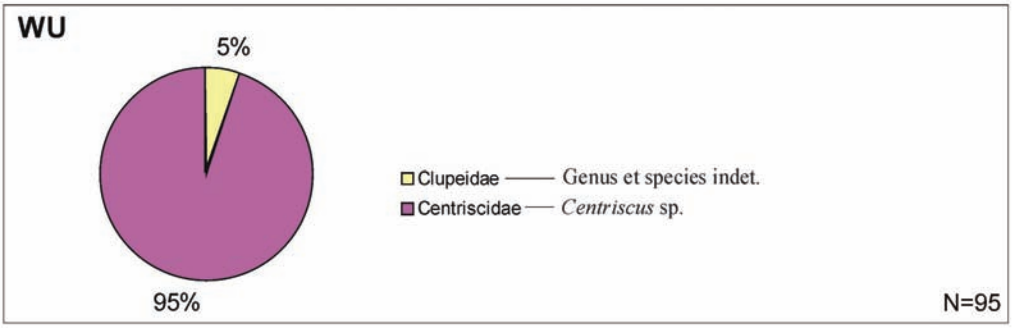
Fish skeletons in each of the ichthyotaphocoenoses are heavily compressed. In ichthyotaphocoenoses RU.34, RU.32, RU.WAP1, RU.WAP2 and WO, the skeletal elements are well preserved, very hard, and keep their original shape. Their surface is bright (grey or brown) and the fracture is either white matt or brown vitreous. Locally, they are translucent. In thin sections their colour is variable, depending upon the section view (Text-fig. 7B, C). In the remaining ichthyotaphocoenoses, the skeletal elements are very poorly preserved or totally damaged. Imprints containing only a brown or black residue of bones are common. If bones are preserved, they are fragile; in thin sections they tend to be black (Text-fig. 7A) or dark brown. Diagenetic processes caused dissolution of all carbonate skeletal elements, primarily aragonite otoliths, which are absent in all of the specimens studied. The soft



Text-fig. 11. Taxonomic composition of ichthyotaphocoenoses RU.WAP2, RU.WAP1, RU.32, RU.34 from the locality Rudawka Rymanowska; N – number of specimens examined



Text-fig. 12. Taxonomic composition of ichthyotaphocoenose WO from the locality Wola Czudecka; N – number of specimens examined



Text-fig. 13. Taxonomic composition of ichthyotaphocoenose WU from the locality Wujskie; N – number of specimens examined

body outline, visible in many specimens, is due to the presence of scales and/or dark-coloured organic matter (Text-figs 14A, B; 28A, D; 36B). In the orbit region, or within the body outline, dark concentrations are commonly found of most probably originally putrid matter that orginated during the decay of organic matter (see Berner 1968; Matyja 1978). Sometimes, the luminous organs (photophores) may be observed as dark points or circular pits on the scales. They are conspicuous in some specimens of the families Phosichthyidae and Myctophidae from ichthyotaphocoenoses JD1.B and JD1.C (see Jerzmańska 1968). Two specimens with photophores are preserved in the ichthyotaphocoenose WO; the first is a representative of the family Myctophidae, the second of the Phosichthyidae. Luminous organs have been reported quite often in deep sea fishes from other Oligocene deposits of the Outer Carpathians (see Jerzmańska 1960, 1968), having been noted in the families Gonostomatidae (genus *Scopeloides)*, Phosichthyidae (genus *Vinciguerria*), Myctophidae (genus *Eomyctophum*), and Sternoptychidae (genus *Polyipnus*).

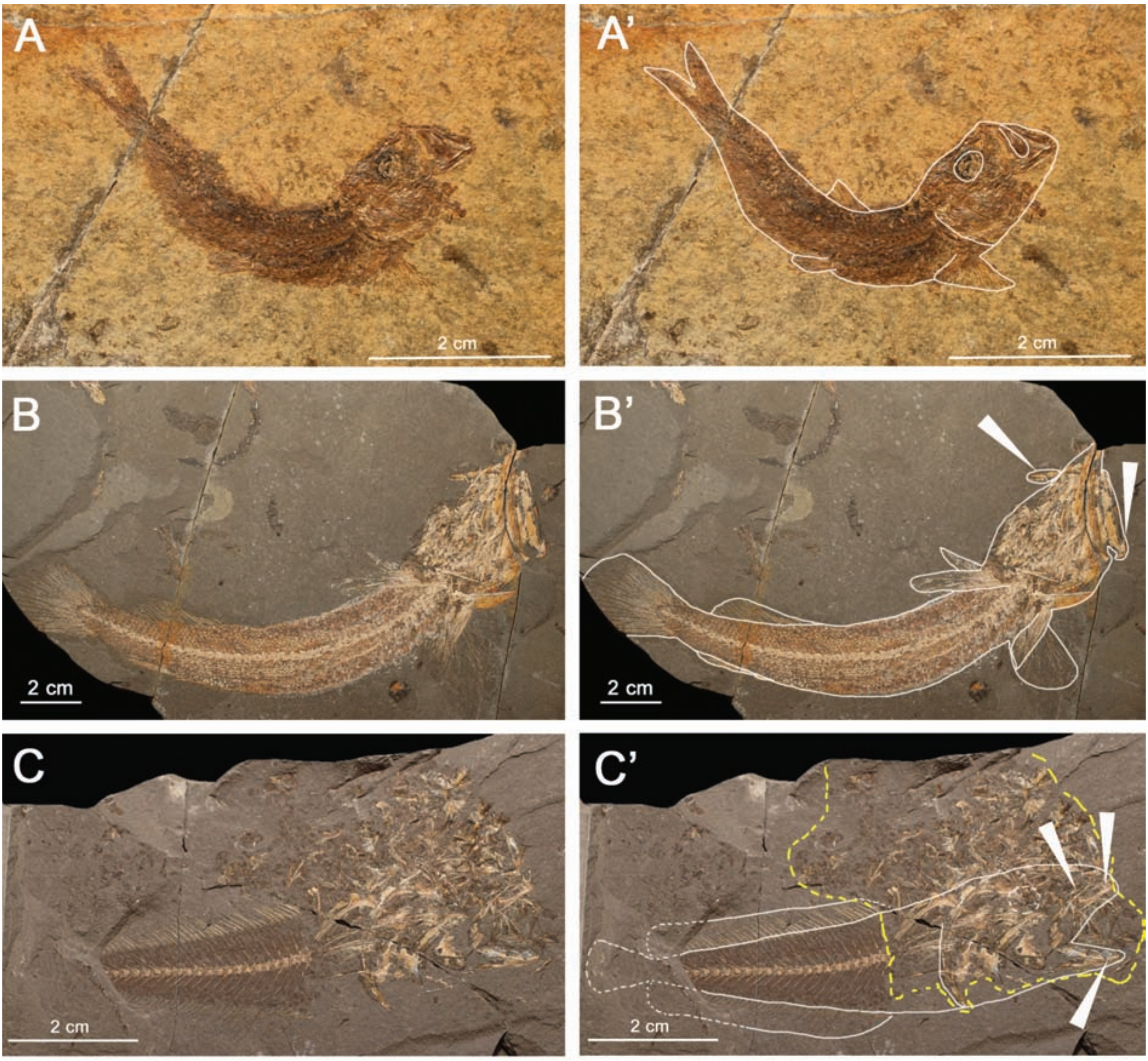
Degree of skeleton disarticulation

The degree of skeleton disarticulation was estimated using methods comparable to those used by McGrew (1975) and Wilson and Barton (1996). Each specimen was coded as belonging to one of the five stages of disarticulation: (1) stage 5 (very well preserved) – skeleton completely articulated (e.g. Text-fig. 18A); (2) stage 4 (well preserved) – skeleton slightly disarticulated, a few skeletal elements displaced or missing (e.g. Text-fig. 14B); (3) stage 3 (moderately preserved) – skeleton distinctly disarticulated (semi-articulated), half or more of skeleton articulated; pattern of preservation variable: usually disarticulated are skull bones (Text-fig. 14C) and scales from the abdominal portion of the skeleton (Text-fig. 15A); (4) stage 2 (poorly preserved) – less than a half of skeleton articulated (e.g. Text-fig. 15B); and (5) stage 1 (very poorly preserved) – scattered skeletal elements of one individual (e.g. Text-fig. 15C), or only a few bones articulated.

Based on the percentage share of particular preservational groups (see Text-figs 16 and 17) the ichthyotaphocoenoses are subdivided into three groups: Group 1 (JD1.B, JD1.C, JD1.D, JD1.E, JD1.E1), with a high percentage of skeletons of stage 3; Group 2 (RU.WAP1, RU.WAP2), with the majority of skeletons of stage 5; and Group 3 (RU.32, RU.34), with a high percentage of skeletons of stages 3 and 5.

Outside these groups is ichthyotaphocoenose WU.1, characterised by a high percentage of poorly preserved skeletons of stage 1.

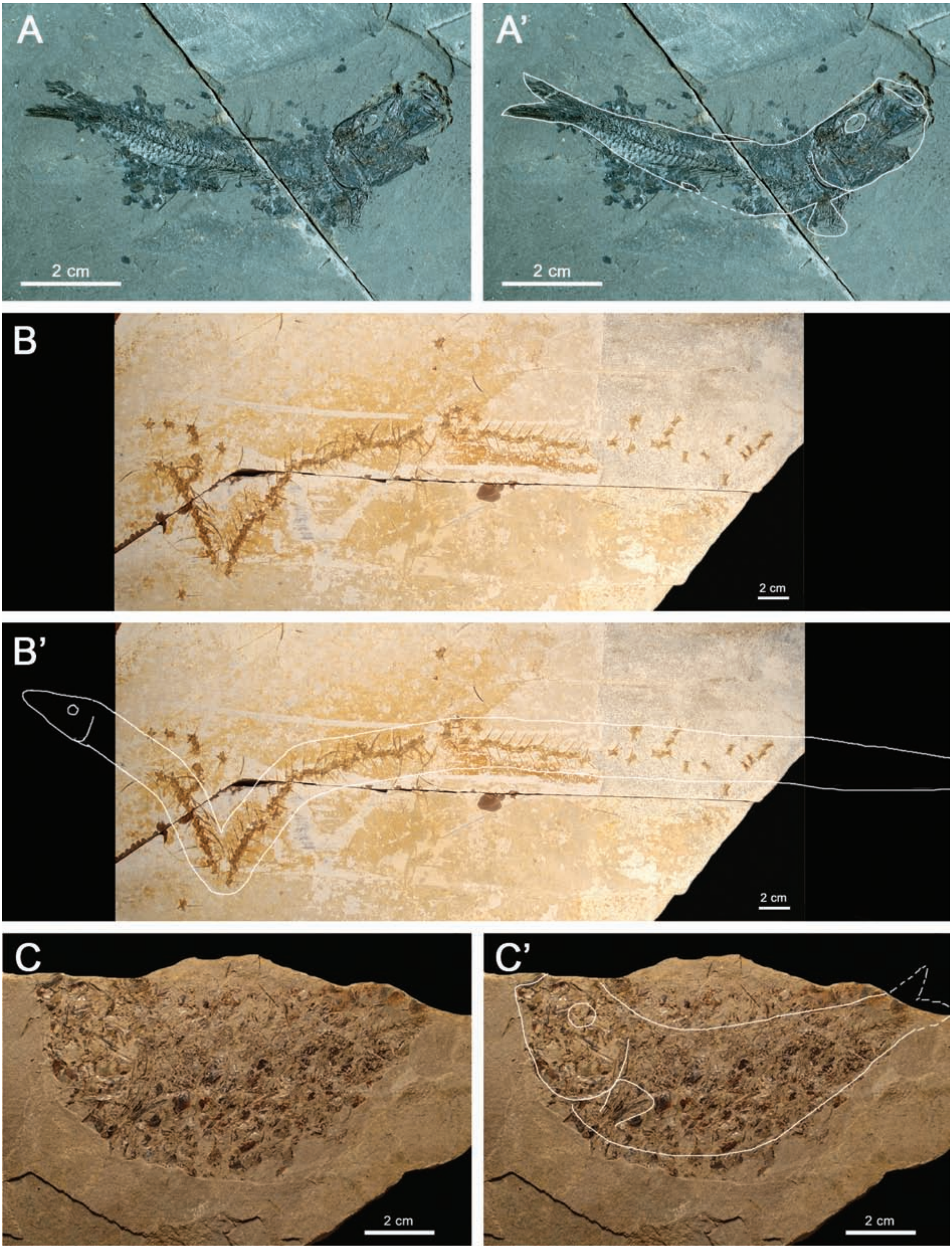
Histograms of the state of skeleton disarticulation showing the number of specimens of each family (Text-figs 18–20) illustrate that preservational conditions of



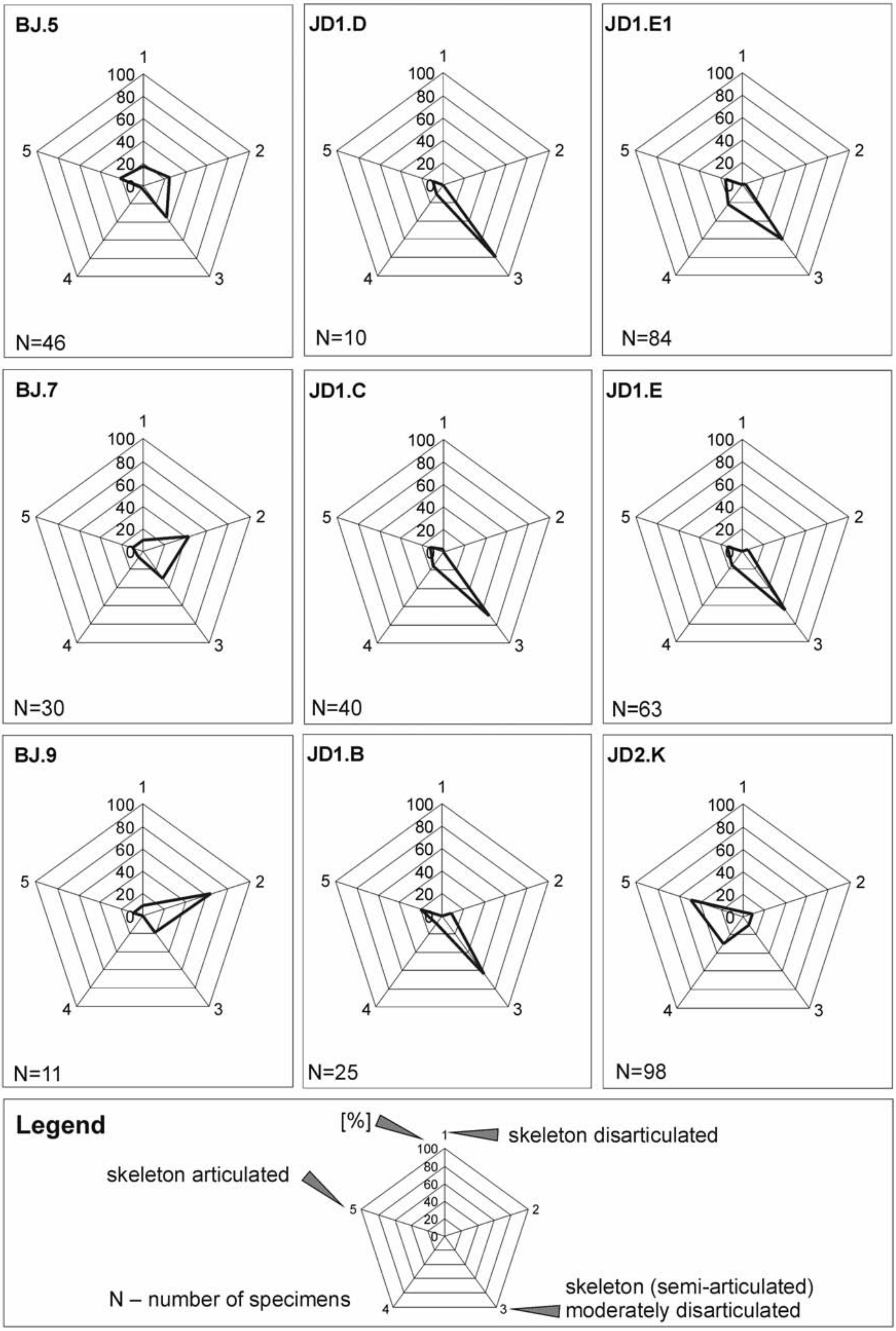
Text-fig. 14. Stages of skeleton disarticulation illustrated by examples: **A**,**A'** – Stage **5** (very well preserved, articulated), Clupeidae, locality Rudawka Rymanowska (layer WAP1); **B**,**B'** – Stage **4** (well preserved), arrows indicate displaced bones of skull, Merlucciidae, Rudawka Rymanowska (layer 34); **C**,**C'** – Stage **3** (moderate), skeletal elements of the anterior part of the skeleton are disarticulated (yellow outline) and most of them are slightly displaced, jaw bones (arrow) are close to anatomical position, Merlucciidae, Rudawka Rymanowska (layer 34)

a selected family are unrepresentative for the whole ichthyotaphocoenose. For instance, skeletons of the Sternoptychidae are only moderately and very well preserved (Text-fig. 21), whereas other skeletons fall into all stages of disarticulation. Fish carcasses of different families, as was indicated by Schäfer (1972) in experiments on carcasses of Recent fishes, are more or less susceptible to factors leading to disarticulation. Carcasses of the Clupeidae lose their scales soon after death (Weiler 1929), whereas the Syngnathidae do so after 23 days in well-aerated sea water at a temperature of 15°C, at an advanced stage of body decomposition (Schäfer 1972, pp. 56 and 82). Apart from the Syngnathidae, the Sternoptychidae are probably also very resistant to disarticulation, as their skeletons remain better preserved than those of other families. The Centriscidae could also be very resistant to disarticulation, as can be presumed from their resemblance to the Syngnathidae in carrying a body armour of thick scales. Taking into account that variability in the anatomy of fishes may cause different sequences of disarticulation of skeletal elements after death (see Schäfer 1972), the ichthyotaphocoenoses were compared here by an analysis of the state of skeleton disarticulation of selected families.

With regard to the frequencies of states of skeleton disarticulation of the selected families, ichthyotaphocoenoses are similar:

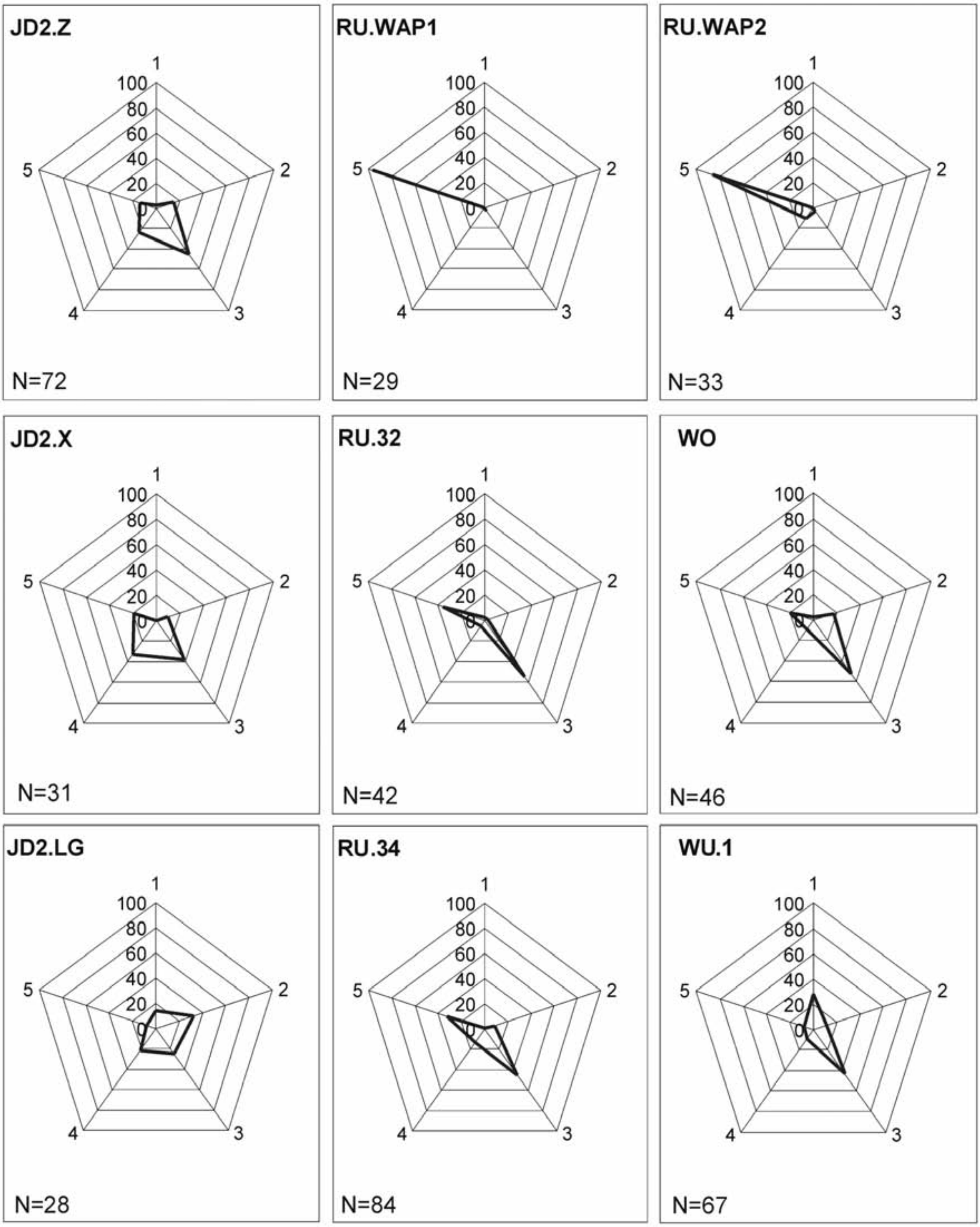


Text-fig. 15. Stages of skeleton disarticulation, illustrated by examples: **A**,**A'** – Stage **3** (moderate), disintegrated abdominal portion of skeleton, some displaced scales present, skull articulated, jaws agape, Clupeidae, locality Jamna Dolna 2 (layer LG); **B**,**B'** – Stage **2** (poorly preserved), less than half of the skeleton articulated, Trichiuridae, locality Wola Czudecka (unit WO); **C**,**C'** – Stage **1** (very poorly preserved), concentration of skeletal elements, some of them articulated, Clupeidae, locality Wujskie (layer 2)

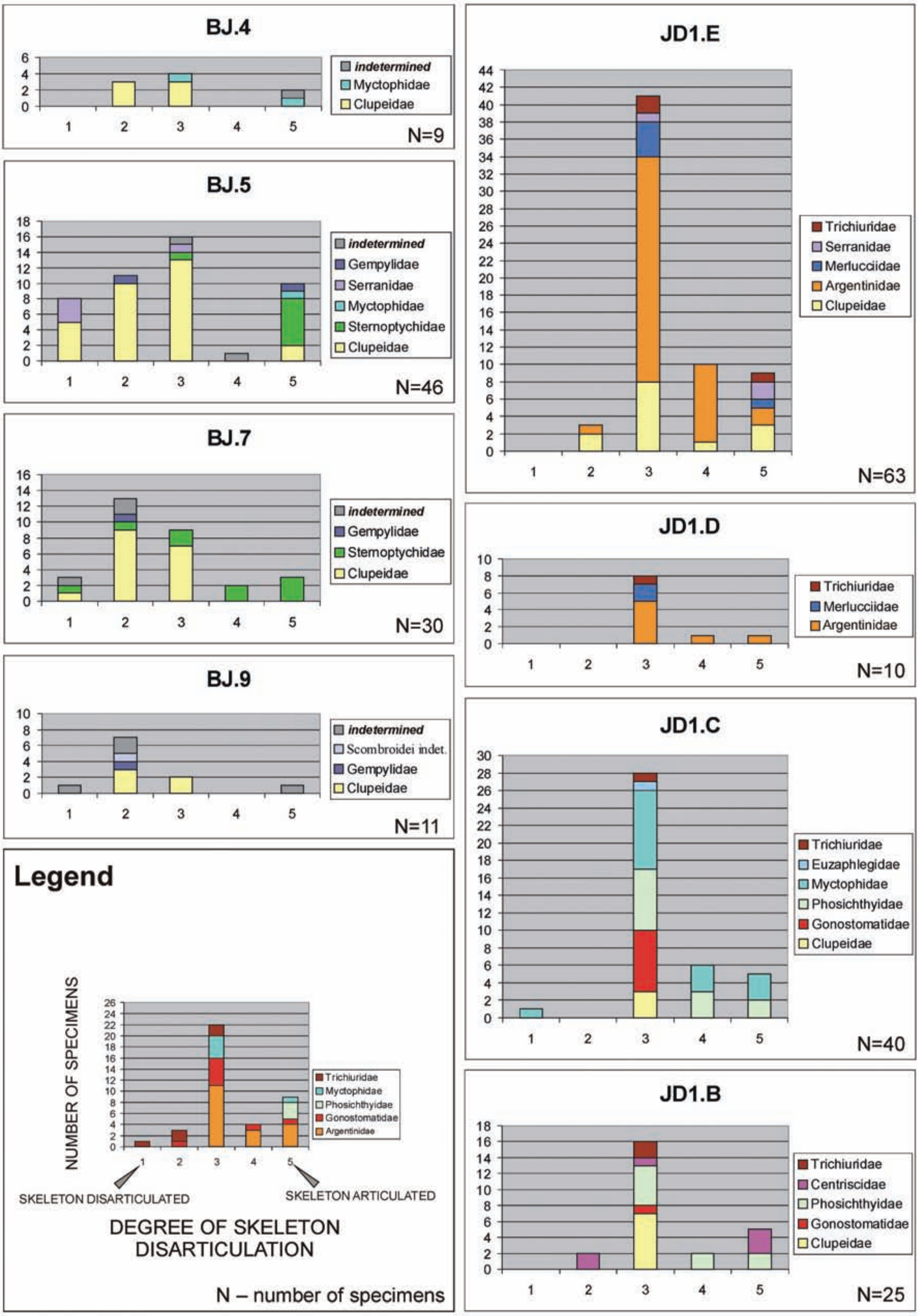


Text-fig. 16. Percentage of each stage of skeleton disarticulation in ichthyotaphocoenoses: BJ.9, BJ.7, BJ.5, JD1.B, JD1.C, JD1.D, JD1.E, JD1.E1, JD2.K

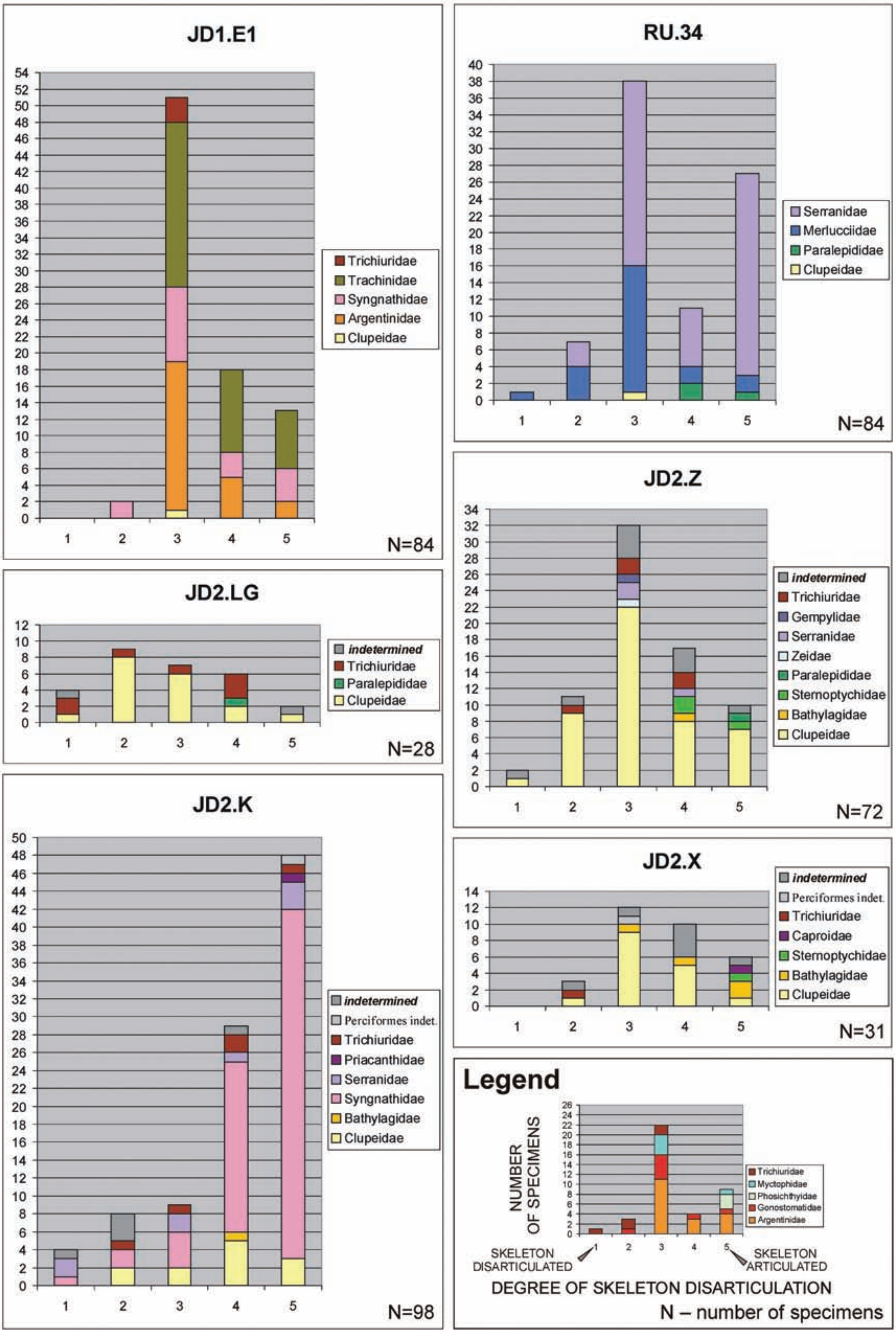
- RU.32 and RU.34 for the Merlucciidae (Text-figs 19 and 20);
- RU.32 and RU.34 for the Serranidae (Text-figs 19 and 20);
- JD2.X, JD2.Z and JD1.E for the Clupeidae (Text-fig. 22A);
- JD1.E1, JD1.E, JD1.D and WO for the Argentinidae (Text-fig. 23A);
- JD1.C and JD1.B for the Phosichthyidae (Text-fig. 18);
- BJ.7 and BJ.5 for the Clupeidae (Text-fig. 22A), and probably (because of some indistinct differences and



Text-fig. 17. Percentage of each stage of skeleton disarticulation in taphocoenoses: JD2.LG, JD2.X, JD2.Z, RU.34, RU.32, RU.WAP1, RU.WAP2, WO, WU.1; legend as for Text-fig. 16



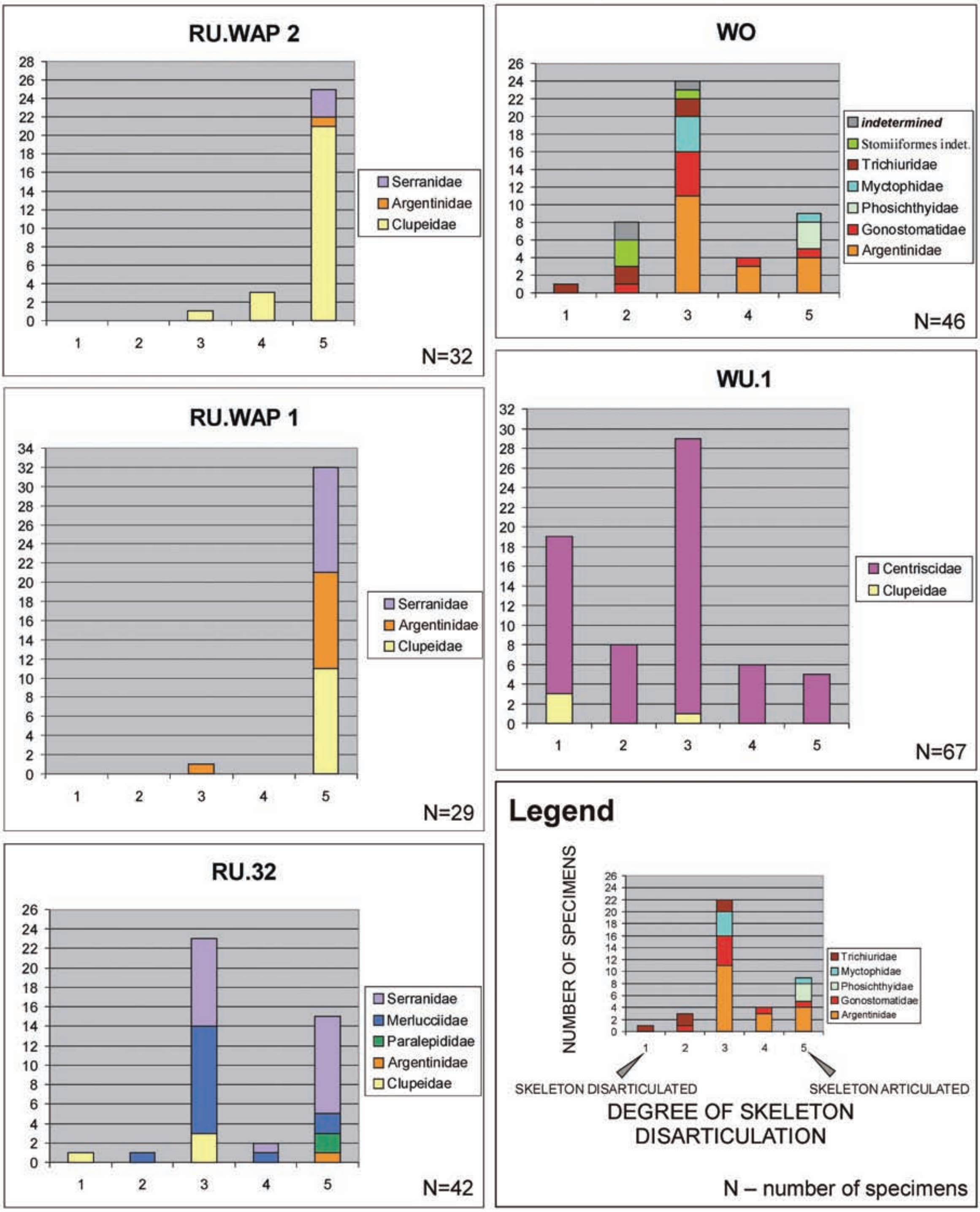
Text-fig. 18. Frequencies of stages of skeleton disarticulation, with taxonomic assignment, in ichthyotaphocoenoses: BJ.9, BJ.7, BJ.5, BJ.4, JD1.B, JD1.C, JD1.D, JD1.E



Text-fig. 19. Frequencies of stages of skeleton disarticulation, with taxonomic assignment, in ichthyotaphocoenoses: JD1.E1, JD2.K, JD2.LG, JD2.X, JD2.Z, RU.34

a small number of specimens) also BJ.9, BJ.4 and JD2.LG (Text-figs 18 and 22A); on the other hand, it is unlikely that the slightly better state of skeleton disarticulation of the Clupeidae (Text-fig. 22A), and Sternoptychidae (Text-fig. 22B) in BJ.5 than in BJ.7 is fortuitous.

The state of skeleton disarticulation of the family Syngnathidae (Text-fig. 23B) in ichthyotaphocoenose JD2.K is different from that in JD1.E1. Ichthyotaphocoenose JD2.K contains a high proportion of articulated (stage 5) and well preserved (stage 4) skeletons. In ichthyotaphocoenose JD1.E1, moderately preserved



Text-fig. 20. Frequencies of stages of skeleton disarticulation, with taxonomic assignment, in ichthyotaphocoenoses: RU.32, RU.WAP1, RU.WAP2, WO, WU.1

(stage 3) skeletons are the most numerous. The state of skeleton disarticulation of the family Clupeidae in JD2.K is different from that in BJ.7, BJ.5, RU.WAP1, RU.WAP2, JD2.LG, JD2.X, JD2.Z and JD1.E (Text-fig. 22A). Ichthyotaphocoenose JD2.K is dominated by well preserved (stage 4) skeletons; BJ.5, JD1.E, JD2.Z and JD2.X are dominated by moderately disarticulated (stage 3) skeletons; RU.WAP2 and RU.WAP.1 by articulated (stage 5) skeletons; BJ.7 and JD2.LG contain the highest proportion of poorly preserved (stage 2) skeletons.

State of preservation of disarticulated skeletons

Three states of preservation of disarticulated skeletal elements are distinguished:

A – All skeletal elements are associated with the articulated portion of the skeleton (see Text-figs 14B, C; 15A, C; 25A, C),

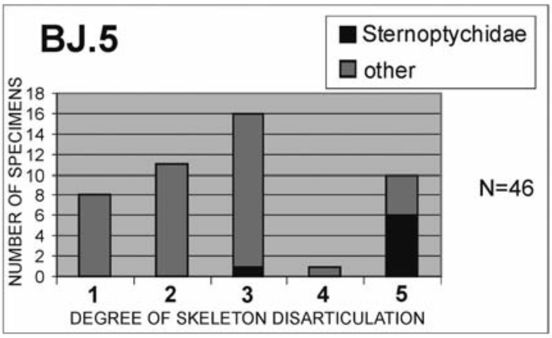
B – Skeletal elements associated with only one articulated portion of the skeleton, but missing in the other (see Text-figs 25B, 40),

C – Many skeletal elements absent, and only a few skeletal elements present close to the articulated portion of the skeleton (see Text-fig. 24B), or isolated skeletal elements are totally absent near articulated portion of the skeleton (see Text-fig. 24A).

State A was observable once in RU.WAP1, where only a single skeleton was found disarticulated, twice in RU.WAP2, and commonly in all of the other ichthyotaphocoenoses (Text-fig. 44).

State B was observable rarely (Text-fig. 44) in ichthyotaphocoenoses BJ.9, BJ.4, JD1.B, JD1.C, JD1.D, JD1.E, JD1.E1, JD2.K, JD2.X, RU.34, RU.32 and WO. This state was observed commonly in ichthyotaphocoenoses BJ.7, BJ.5 and JD2.Z in representatives of the family Clupeidae.

State C is recognized when a portion of the skeleton is articulated (e.g. skull), while skeletal elements of its remaining portion are absent (see Text-fig. 24A), when a small part of the skeleton is articulated and associated with a few scattered/displaced elements (see Text-fig. 24B), or when skeletal elements of a portion of the skeleton are disarticulated and scattered. State C was rarely observed in ichthyotaphocoenoses BJ.9, JD1.B, JD1.C, JD1.E, JD1.E1, JD2.K, JD2.LG, JD2.X, JD2.Z, RU.32, RU.34, RU.WAP1, WO and WU.1. State C was commonly observed in BJ.5 and BJ.7; it constitutes 30% in BJ.5 and 22% in BJ.7. Most of the specimens included in state C in the last two ichthyotaphocoenoses are representatives of the family Clupeidae. Specimens which belong to state C are represented by a portion of the skeleton in various states of preservation, ranging from very well preserved (articulated, see Text-fig. 24A) to completely disarticulated.



Text-fig. 21. State of skeleton disarticulation of the family Sternoptychidae and other fishes in ichthyotaphocoenose BJ.5; N – number of specimens examined

Two types of arrangement of skeletal elements in relation to the articulated portion of the skeleton are recognized here: situated close to the articulated portion (type 1); situated at a distance from the articulated portion (type 2).

Type 1 (see Text-figs 14B, C; 15A, C; 25C) was observable in each of the ichthyotaphocoenoses (see Text-fig. 44).

Type 2 (see Text-fig. 25A) was observable rarely in ichthyotaphocoenoses BJ.5, JD1.B, JD1.E, JD2.K, JD2.X, JD2.Z, RU.34, RU.32 and WO (Text-fig. 44).

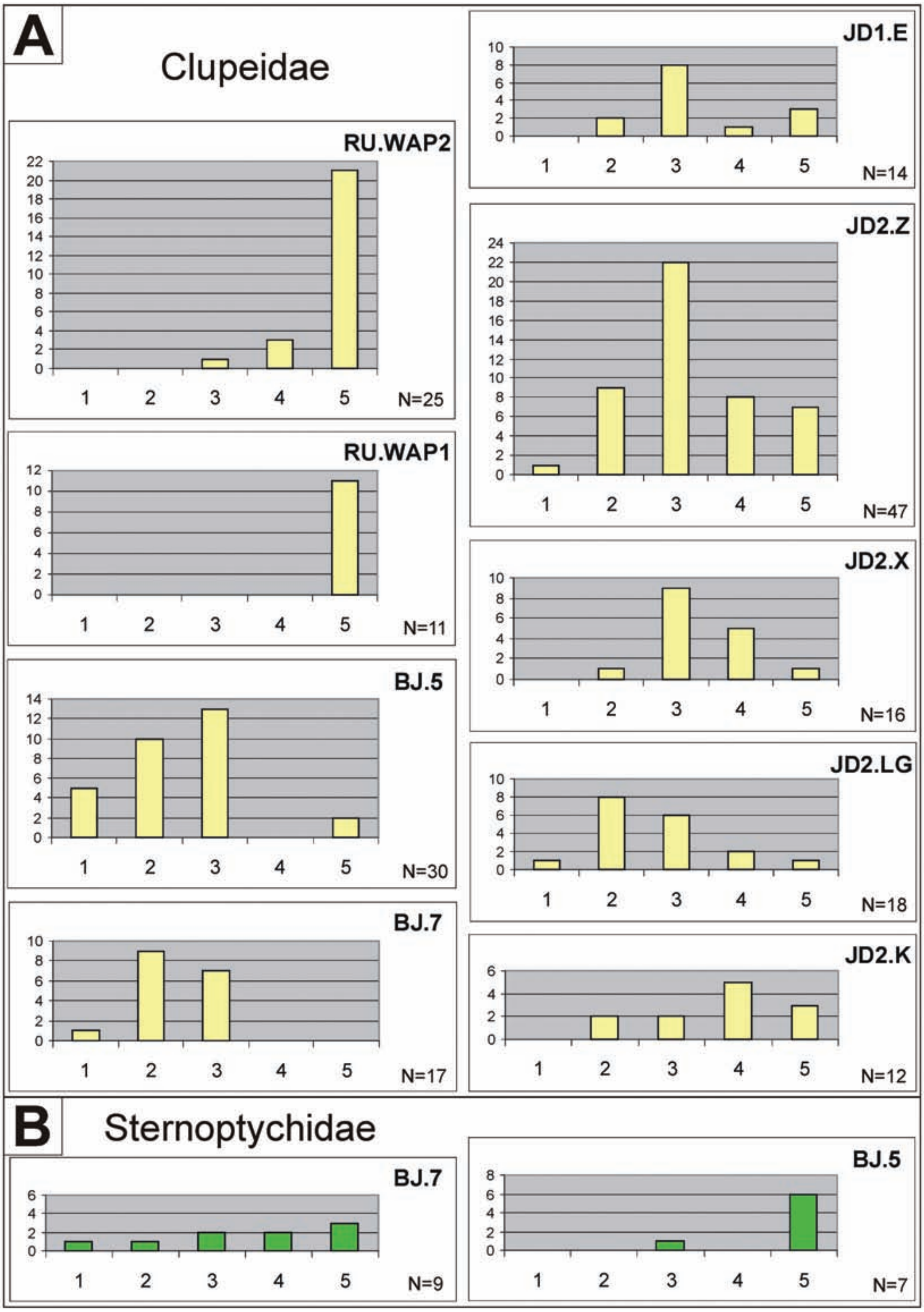
Spatial arrangement of skeletons

The direction of the long axis of each fish skeleton that shows a straight or slightly arched vertebral column was measured on bedding planes. In ichthyotaphocoenoses JD2.K and RU.34, which yielded 107 and 52 measurements respectively, the orientation of the fish skeletons is random (see Text-fig. 26); in ichthyotaphocoenoses WU.1 (N=27; N – number of measurements), WO (N=17), and BJ.5 (N=17) there is also no preferred orientation.

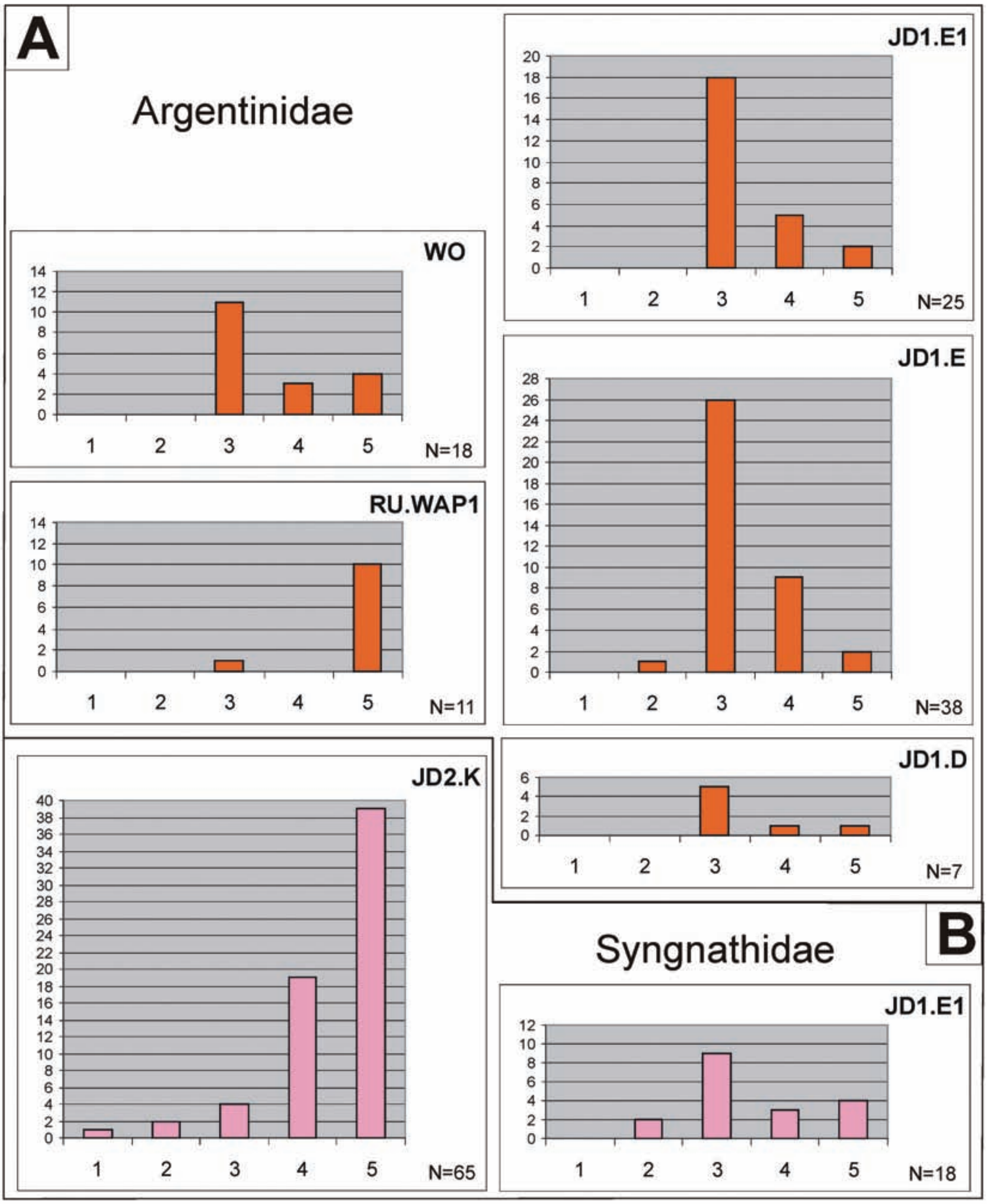
State of preservation of vertebral column, fins, and jaws

Observations were made on articulated parts of the skeleton. Six types of vertebral column preservation are easily recognized: straight (undeformed), curved (arched, in an *S*-shape, in a circle, irregular), and broken.

Generally, the vertebral column of fishes of a given family, and of similar body shape, is deformed in a characteristic pattern. The vertebral column tends to be straight when the body is short and deep, as shown by specimens of the families Zeidae, Sternoptychidae (Text-fig. 28B) and Serranidae (Text-fig. 28A). It is variably preserved if the body is moderately elongate and narrow, as shown by specimens belonging to the families Gonostomatidae, Trachinidae, Merlucciidae, Phosichthyidae, Myctophidae, Bathylagidae, Clupeidae and Argentinidae. It tends to be curved in specimens of the families Bathylagidae, Clupeidae and Argen-



Text-fig. 22. State of skeleton disarticulation: **A** – Clupeidae, in ichthyotaphocoenoses: BJ.7, BJ.5, JD1.E, JD2.K, JD2.LG, JD2.X, JD2.Z, RU.WAP1, RU.WAP2; **B** – Sternoptychidae, in ichthyotaphocoenoses: BJ.7, BJ.5; horizontal axis – stages of skeleton disarticulation, vertical axis – number of specimens, N – total number of specimens examined tinidae, indicating its high susceptibility to deformation. The state of preservation of the vertebral column in each of the above-listed families is concordant with Weiler's (1929) opinion that *post-mortem* contortions tend to appear in fishes with narrow bodies. The type of preservation of the axial skeleton of fishes of the families Centriscidae and Syngnathidae is an exception to Weiler's opinion. The anatomy of these fishes is distinctly different from that of the other fishes examined. Their vertebral column is not strongly deformed, because they carry a body armour of thick scales which strengthens/stiffens their skeleton. The axial skeleton of the razorlike-bodied Centriscidae (Text-fig. 37) is mostly undeformed (apart from one specimen), whereas in the very elongate and narrow Syngnathidae (Text-fig. 28C) it is slightly arched or straight. The most common curvatures displayed by the representatives of particular families are as follows:

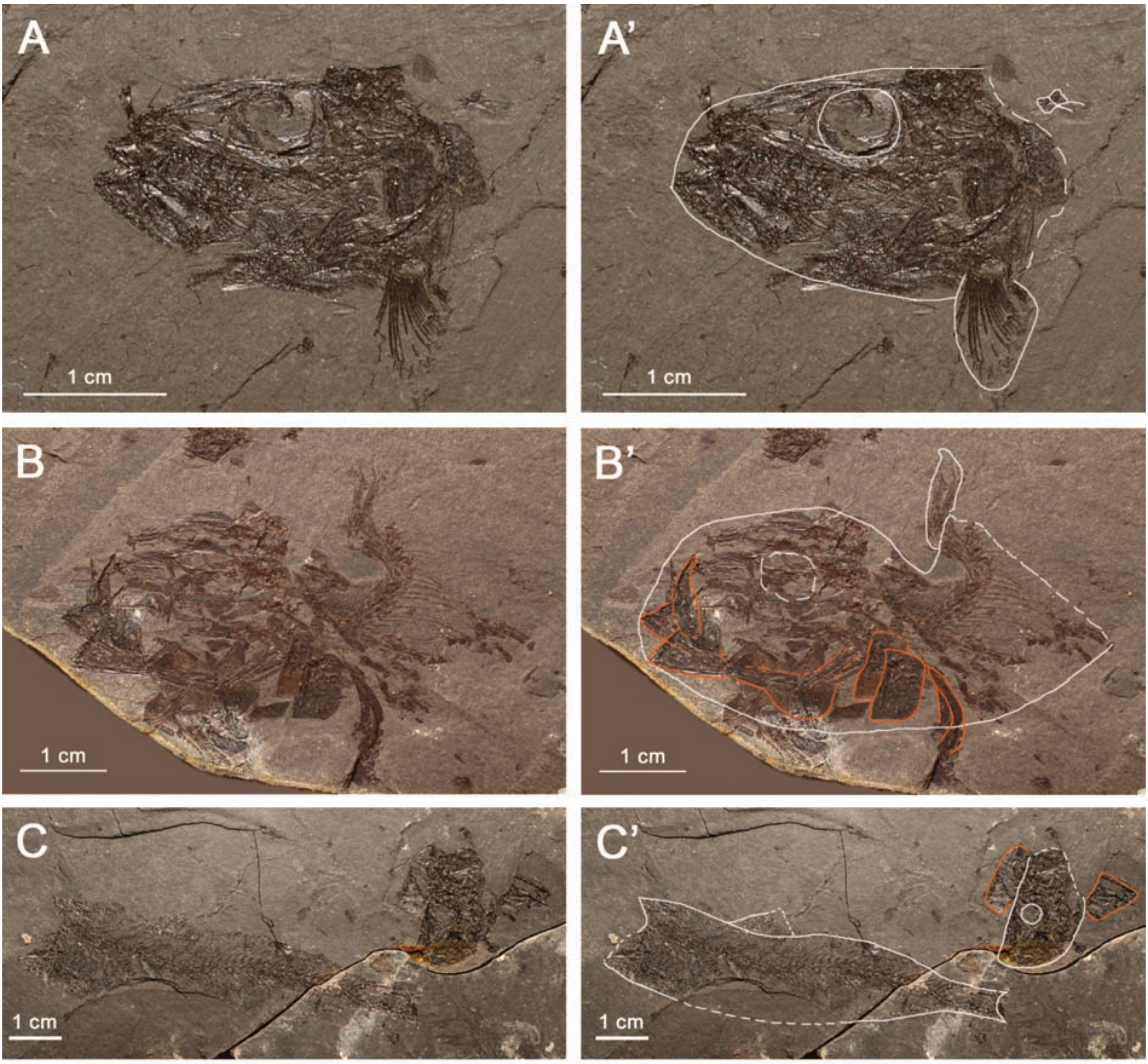


Text-fig. 23. State of skeleton disarticulation: **A** – Argentinidae, in ichthyotaphocoenoses: JD1.D, JD1.E, JD1.E1, RU.WAP2, WO; **B** – Syngnathidae, in ichthyotaphocoenoses: JD1.E1, JD2.K; horizontal axis – stages of skeleton disarticulation, vertical axis – number of specimens, N – total number of specimens examined

- Sternoptychidae – slightly arched or curved irregularly in the posterior part of the vertebral column;
- Serranidae – slightly arched;
- Gonostomatidae – slightly curved in an *S*-shape or curved irregularly;
- Trachinidae, Myctophidae – slightly arched or curved irregularly;
- Merlucciidae – slightly to moderately arched (Text-fig. 14B);
- Phosichthyidae, Bathylagidae, Clupeidae – from slightly to strongly arched (Text-fig. 14A and 15A), curved in an *S*-shape (Text-fig. 28A) and irregularly;
- Argentinidae – from slightly to strongly arched, curved in an *S*-shape, curved irregularly (Text-fig. 29A, C), and rarely curved in a circle (Text-fig. 29B);
- Syngnathidae – slightly arched (Text-fig. 28C).

A strong curvature of the vertebral column was mostly observable when the skeleton was partially disarticulated. It is exemplified by representatives of the Argentinidae (Text-fig. 27B).

Skeletons with a deformed vertebral column and a detached and displaced caudal fin are very rare. This state of

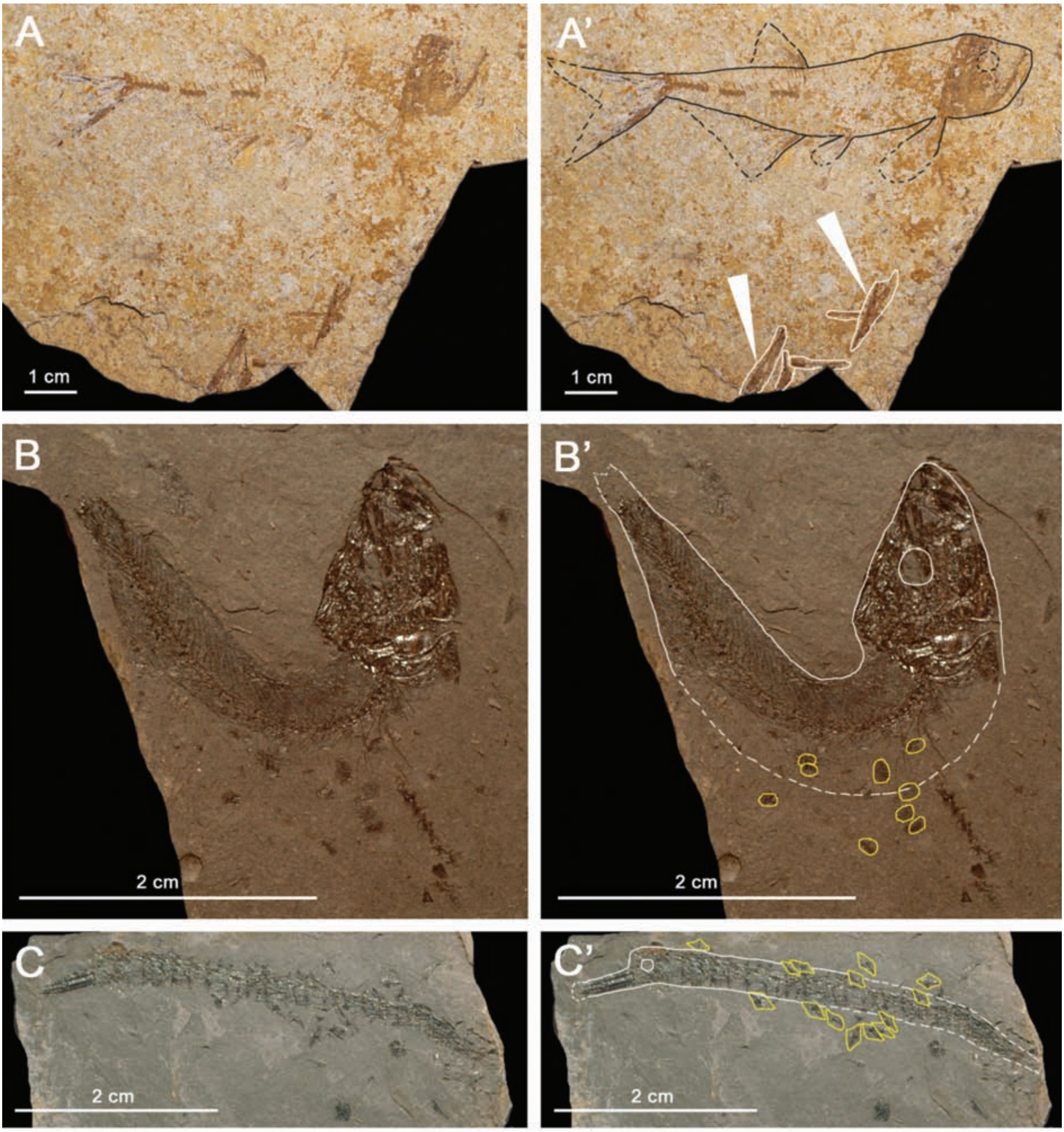


Text-fig. 24. Pattern of skeleton disarticulation exemplified by specimens of the family Clupeidae. **A**,**A'** – Articulated skull with pectoral fin, detached from the rest of the body, locality Błażowa (layer 5), specimen No. BJ.5.31; **B**,**B'** – Skull bones slightly displaced from anatomical position (some outlined by red line) and a fragment of anterior vertebral column, locality Błażowa (layer 7), specimen No. BJ.7.27; **C**,**C'** – Skeleton disintegrated into two pieces: the skull and the rest of the skeleton; a few disarticulated skull bones rest in close proximity to the skull (red outline), locality Jamna Dolna 2 (scree), specimen No. JD2.3

preservation was observable in the following ichthyotaphocoenoses: JD1.E (four specimens), JD1.E1 (four specimens), JD2.Z (a single specimen) and WO (six specimens). The fish from ichthyotaphocoenose JD2.Z is a representative of the family Clupeidae; the other specimens are of the Argentinidae; the vertebral column in all cases is curved either in an *S*-shape (Text-fig. 30), or irregularly.

The state of preservation of the vertebral column for representatives of particular families was compared among ichthyotaphocoenoses containing more than 10 observations (examples) in a family. Similarity is apparent between certain ichthyotaphocoenoses (see Text-fig. 27A):

– BJ.5 and JD2.Z, as demonstrated by individuals of the family Clupeidae,



Text-fig. 25. Pattern of skeleton disarticulation: **A**,**A'** – Specimen of the family Gonostomidae and its mandibular bones (arrowed) at a distance equal to a half length of the skeleton, locality Wola Czudecka (unit WO), specimen No. WO.49; **B**,**B'** – Specimen of the family Clupeidae, with only a few disarticulated scales (yellow outline) resting in spatial proximity to the articulated portion of the skeleton; pectoral fin rays and scales from the abdominal region are absent, locality Jamna Dolna 2 (layer Z), specimen No. JD2.Z.30; **C**,**C'** – Specimen of the family Syngnathidae, scales slightly displaced (yellow outline) rest near the skeleton, locality Jamna Dolna 2 (layer K), specimen No. JD2.K.129

- RU.34 and RU.32, as shown by specimens of the families Merlucciidae and Serranidae,
- JD1.E and JD1.E1, as shown by specimens of the Argentinidae.

Two types of preservation of fins are recognized: with erect rays (fin is fan-shaped; see pectoral fin, Text-fig. 14A) and with reclinate rays (rays are parallel, see dorsal and pelvic fins, Text-fig. 30A). In some cases, one fin can have some rays erect and the rest reclinate. Such a state of preservation is rare in the material presented. Any one of the fins (e.g., dorsal, anal, pectoral or pelvic) of a given individual can display one of these two types of preservation independently of the type of preservation of the other fins, the degree of skeleton disarticulation, the type of preservation of the vertebral column, or even of the jaws.

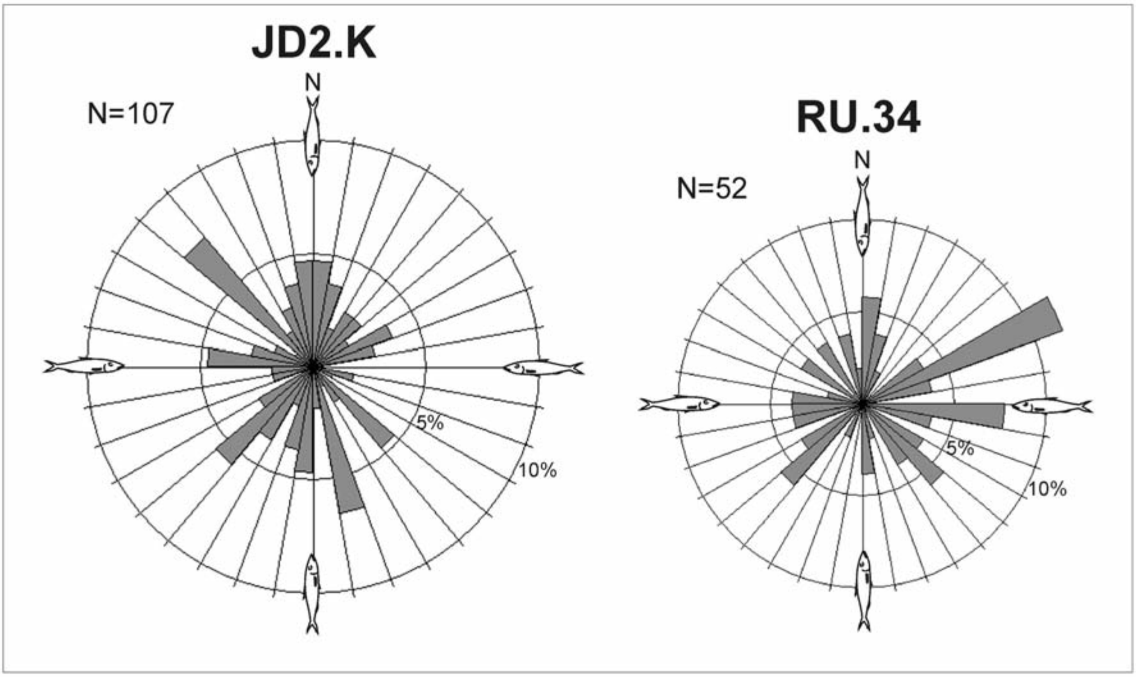
Three types of preservation of jaws are recognized: closed (pressed together), slightly agape, fully agape. Specimens of the families Syngnathidae and Centriscidae were not examined due to difficulty in recognising the type of preservation of their jaws. Jaws both closed and agape were common in ichthyotaphocoenoses RU.34, RU.32, RU.WAP1 and RU.WAP2 (see BIEŃKOWSKA 2004b, fig. 9), JD1.E1 (Text-fig. 31 herein), as well as in JD1.E. A few observations of the other ichthyotaphocoenoses allows only the observation that jaws both closed and agape occur. The presence of jaws agape is irrespective of the vertebral column curvature, or of the preservation (erection) of the fin rays.

Unusual cases of preservation

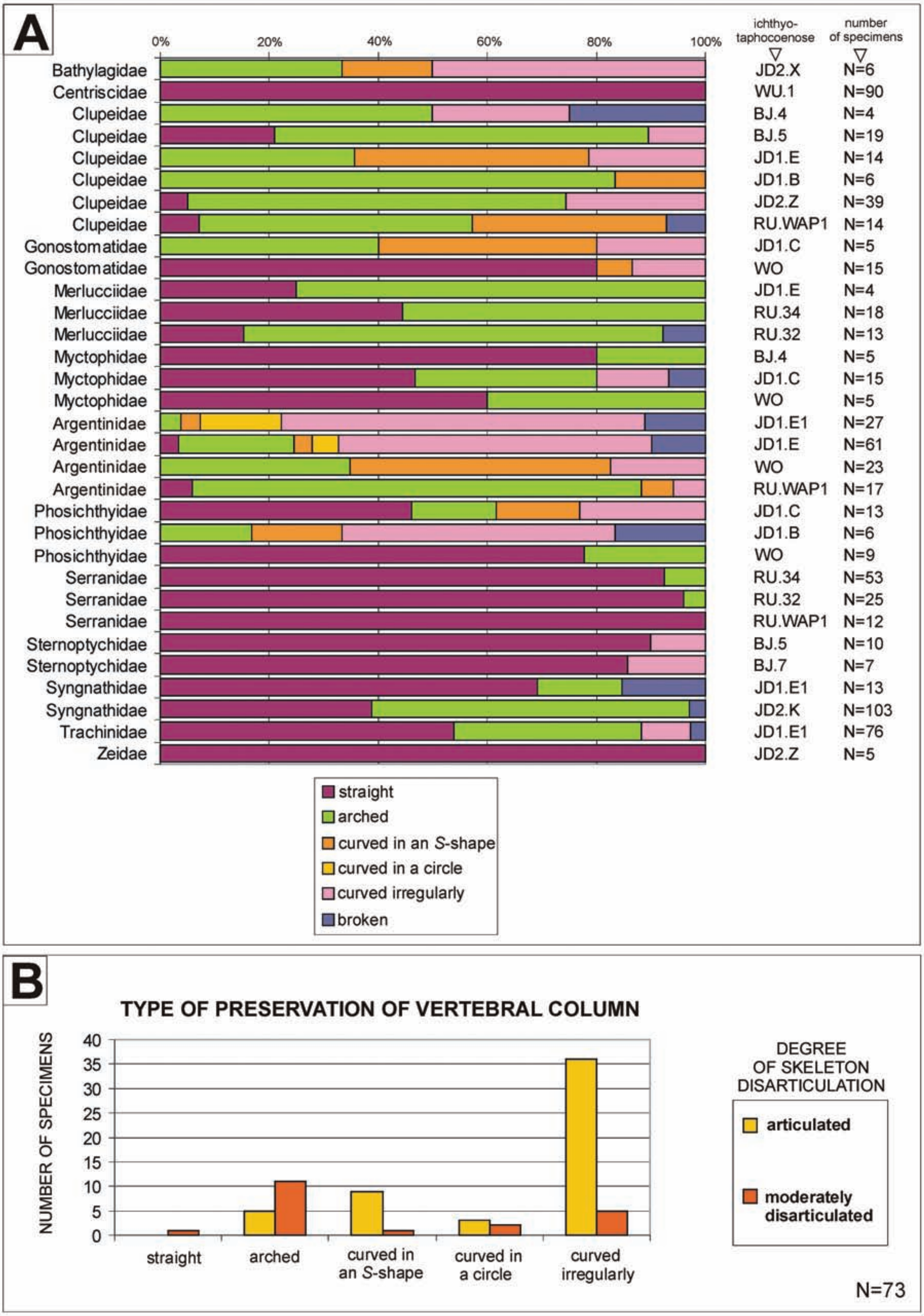
Two unusual cases of preservation were found: (1) the fish that has choked to death on a fish (fish swallowing a smaller one); (2) the fish containing a prey fish in its stomach (fish with a swallowed prey fish).

The first state was noted five times: once in JD1.E1, twice in RU.34, once in RU.32, and once in RU.WAP1. Specimens from RU.34, RU.32 and RU.WAP1 (see Text-figs 32–34) represent fishes (predators and prey) of the family Serranidae. The specimen from JD1.E1 represents (see Text-fig. 35) a predator individual and a prey individual of the species *Trachinus minutus* (JONET, 1958) of the family Trachinidae.

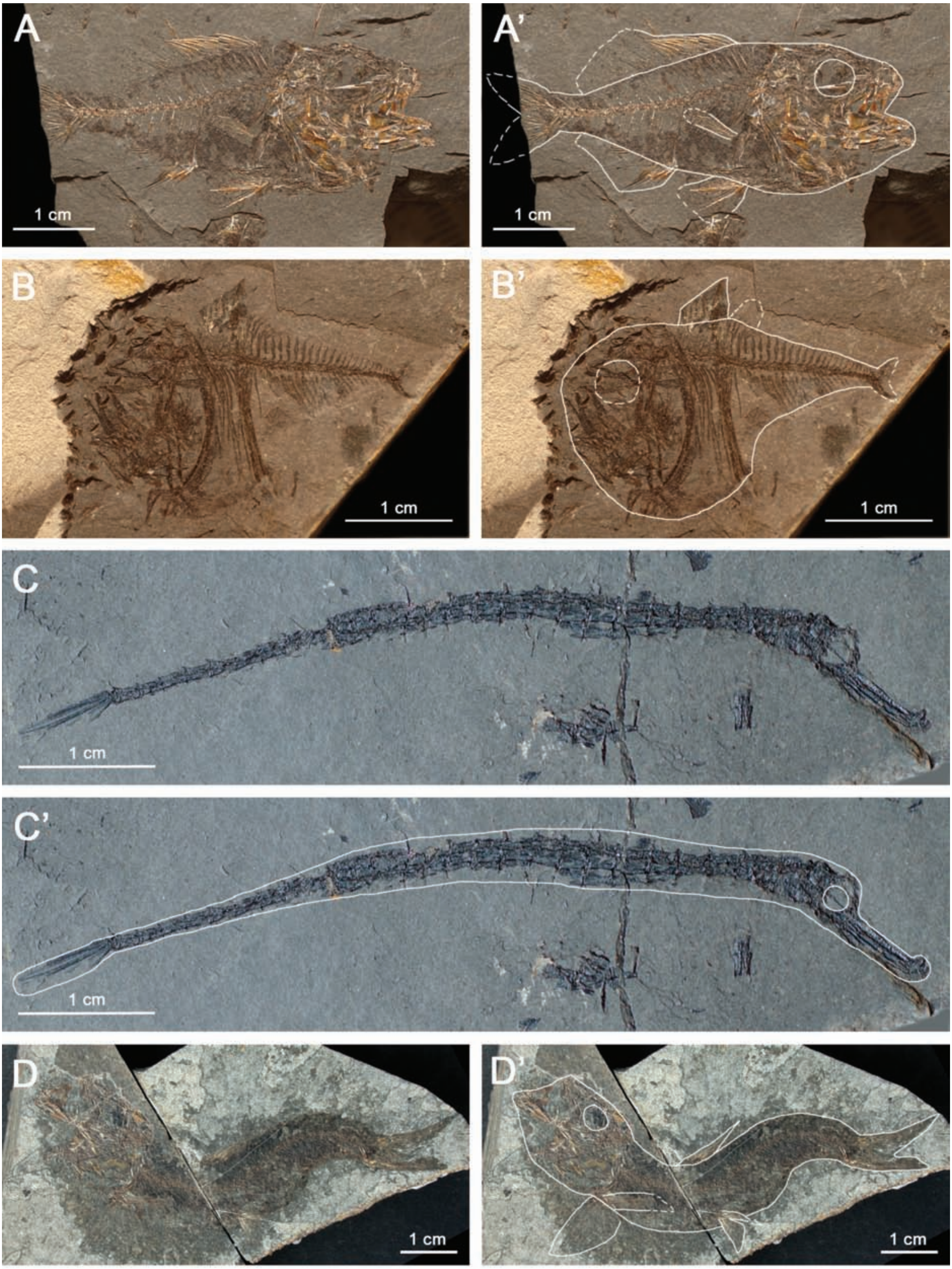
The second case was noted three times: twice in RU.32 and once in RU.34 (Text-fig. 36). The specimen from RU.34 is a new record, while the two specimens from RU.32 have been reported earlier and one of them illustrated (BIEŃKOWSKA 2002, fig. 43 = 2004b, fig. 20). In all cases, the prey individual was swallowed head first (example: Text-fig. 36). A prey individual in all cases has fins with reclinate rays and the vertebral column parallel to the vertebral column of the predator. Each predator is a representative of the species *Holosteus mariae* (Menner, 1948) of the family Paralepididae. One prey individual from RU.32 is a representative of the family Serranidae; the other is undetermined. The single prey individual from RU.34 is a representative of the Argentinidae.



Text-fig. 26. Rose diagram showing directions of long axis of skeletons on bedding planes in ichthyotaphocoenoses JD2.K and RU.34; N – number of measurements



Text-fig. 27. Type of preservation of vertebral column: **A** – Percentage of each type of preservation in families in ichthyotaphocoenoses; **B** – Frequency of types of preservation in the family Argentinidae of skeletons articulated and moderately disarticulated

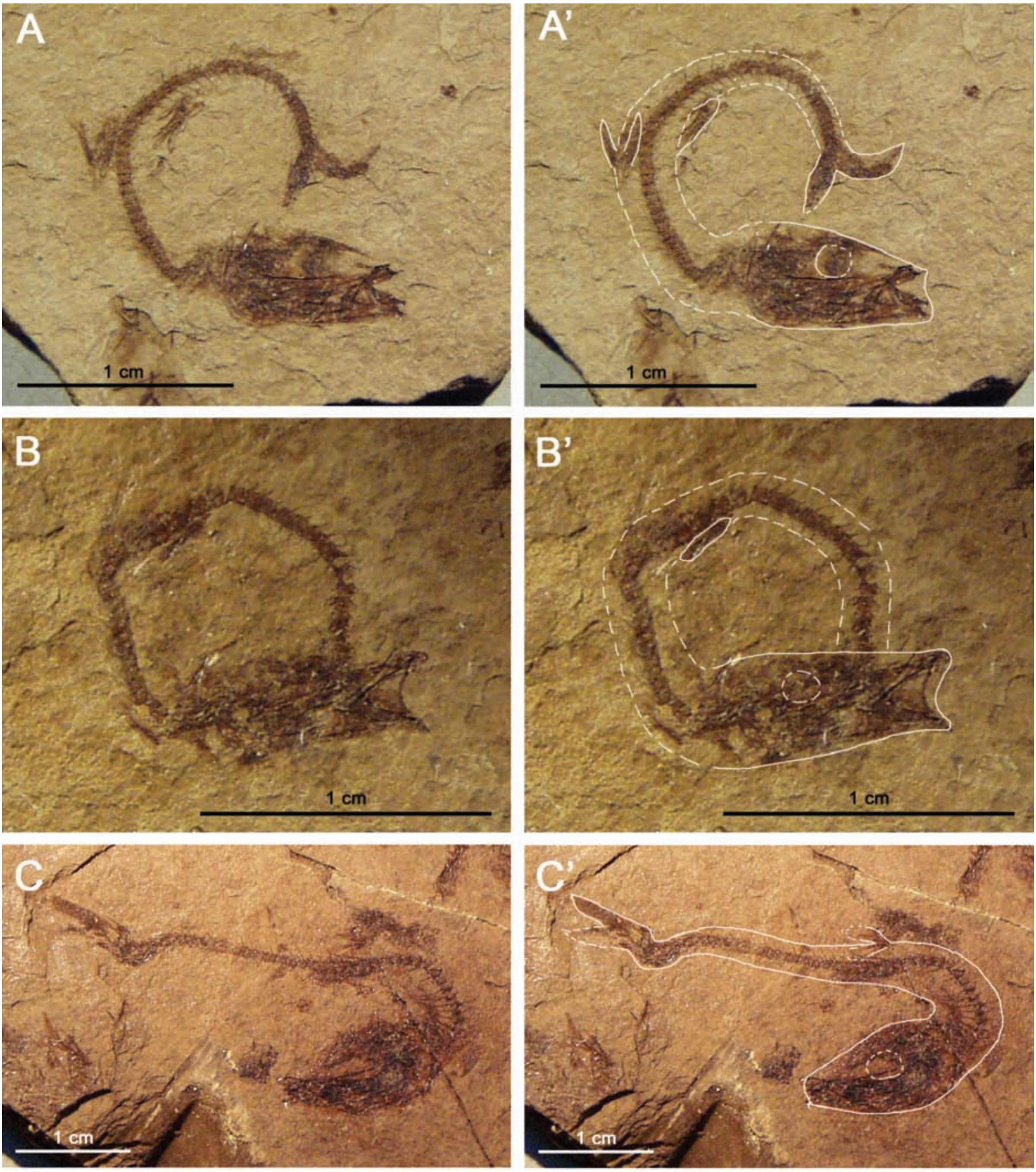


Text-fig. 28. Type of preservation of vertebral column: **A,A'** – Straight, Serranidae, locality Rudawka Rymanowska (layer 34), specimen No. RU01.34.22; **B**,**B'** – Straight, Sternoptychidae, locality Błażowa (layer 7), specimen No. BJ.7.6; **C**,**C'** – Slightly arched, Syngnathidae, locality Jamna Dolna 2 (layer K), specimen No. JD2.K.54; **D**,**D'** – Curved in an *S*-shape, Clupeidae, locality Rudawka Rymanowska (layer WAP1), specimen No. RU03.WAP1.33

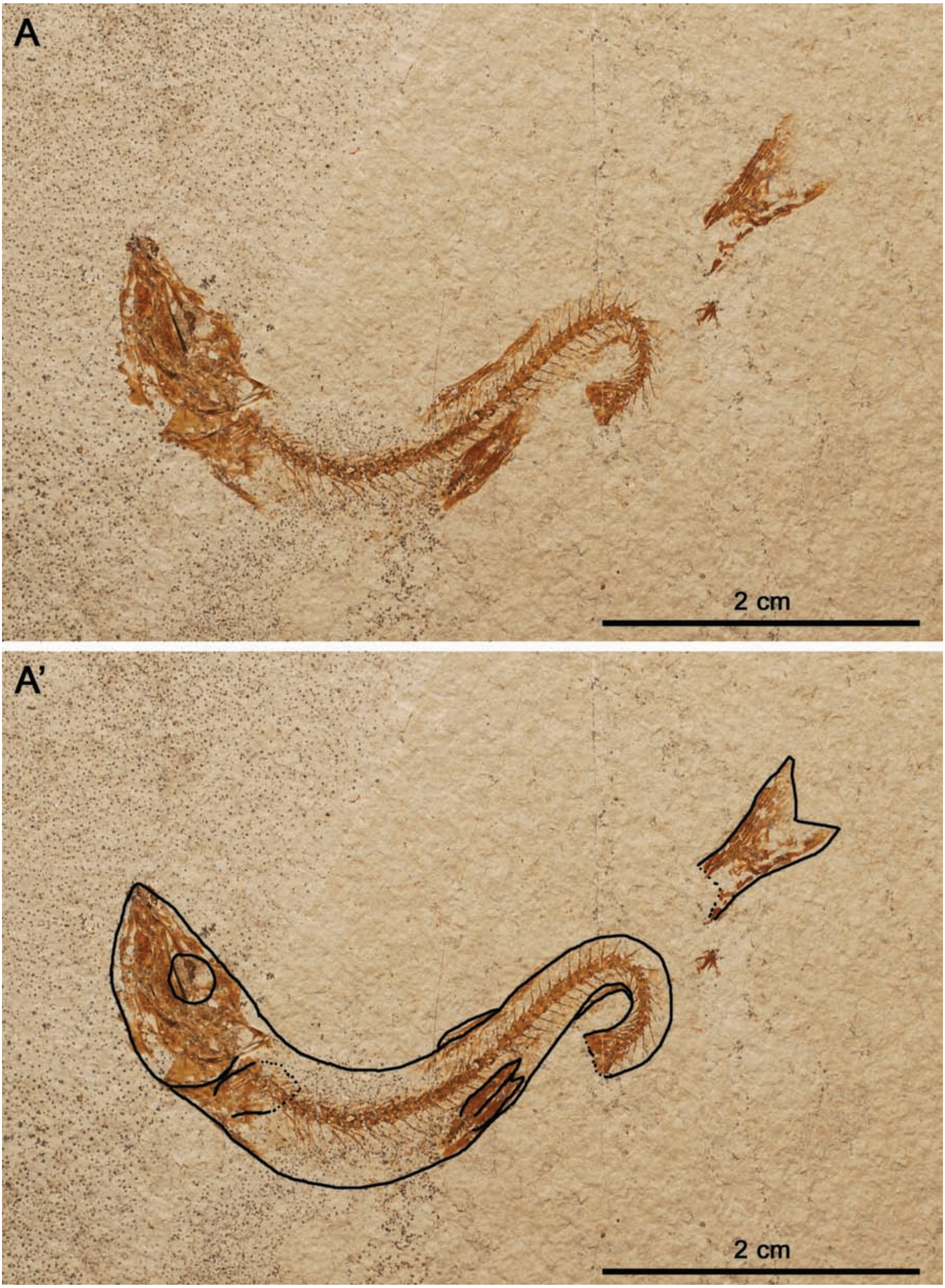
ASSOCIATED FLORA AND FAUNA

In some layers of the Menilite Formation the fish skeletons are associated with remains of other biota.

Terrestrial plant detritus occurs in the localities Błażowa, Jamna Dolna 2, Rudawka Rymanowska and Wola Czudecka, and includes fragments of wood, leaves and twigs. Fragments of wood (Text-fig. 41E, F) occur at Błażowa (layer 5 and 7), Jamna Dolna 2 (layers K, C, LD, P, S, U and Z), Rudawka Rymanowska (presumably in layer WAP1, specimen from the scree), and Wola Czudecka (unit WO). These remains are compressed and carbonized; their size is variable, from slightly



Text-fig. 29. Curvature of vertebral column exemplified by specimens of the family Argentinidae, all from Jamna Dolna 1: **A**,**A'** – Vertebral column curved almost in a circle, (unit E) specimen No. ZPALWr. A/101; **B**,**B'** – Vertebral column curved in a circle, (unit E) specimen No. ZPALWr. A/110; **C**,**C'** – Vertebral column curved irregularly, (layer E1) specimen No. ZPALWr. A/263



Text-fig. 30. Vertebral column curved in an *S*-shape in a specimen of the family Argentinidae (**A**, **A’**), with the caudal fin at a distance from the termination of the vertebral column, indicates a *post-mortem* conversion of arched curvature into an *S*-shaped one; locality Wola Czudecka (unit WO), specimen No. WO.28

more than 0.5 cm to 10 cm in width. The largest specimens measured over 50 cm in length. Some specimens seem to be abraded (Text-fig. 41E, F).

Leaves and fragments of twigs occur at Jamna Dolna 2 (layers D, U and X) and Błażowa (just below layer 5). The leaf at Błażowa was excavated from shales of leaf-like fissility, which also contain fish scales and mica flakes. Normal grading, distinct due to the presence of fish scales and mica flakes, indicates their deposition from a turbidity current. Generally, terrestrial plant detritus is much rarer than the fish skeletons.

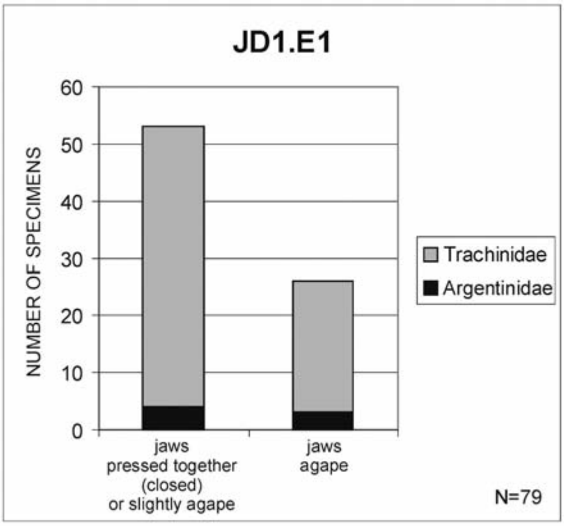
Algae occur in the localities Błażowa, Jamna Dolna 2 and Rudawka Rymanowska. In some layers at Błażowa and Jamna Dolna 2 (Text-fig. 4) they are common. At Rudawka Rymanowska several specimens occurred only below the layer WAP1.

Three morphological types of the algae collected are recognized: (1) filamentous thalli 2–5 mm wide, unbranched or with single dichotomous branching, (2) filamentous thalli 1–3 mm wide with numerous branchings (Text-fig. 41D); (3) filamentous thalli 5–30 mm wide.

Specimens from Błażowa and Jamna Dolna 2 display all three of these morphological types, but the most common are the thalli less than 5 mm wide. Specimens from Rudawka Rymanowska are less than 1.5 cm wide.

Brown algae were formerly noted (Kotlarczyk 1991) at Błażowa in an exposure on the southwestern slope of Wielka Góra.

Some specimens from Jamna Dolna 2 display remains of gas bladders typical of brown algae of the genus *Cystoserites* (see Zastawniak and Worobiec 1997).



Text-fig. 31. Types of preservation of jaws in the families Trachinidae and Argentinidae from ichthyotaphocoenose JD1.E1; N – number of specimens

Marine crabs occur at the localities Błażowa and Jamna Dolna 1. At Jamna Dolna 1, ten specimens of *Portunus oligocenicus* Paucă, 1929, occurred in layer E1 (Jerzmańska 1967b). A single specimen (Text-fig. 43A) is from the upper part of the exposure, approximately at the boundary of units G and H. It shows a strong tooth on the first pair of pereiopods on the carpus, as is typical of *Portunus oligocenicus* (see Jerzmańska 1967b), as well as of *Liocarcinus lancetidactylus* (Smirnov, 1929) (see Garassino and Novati 2001). The state of preservation precludes its reliable taxonomic assignment. A poorly preserved single specimen comes from Błażowa, layer 5. The species *Macropipus oligocenicus* was reported formerly (Kotlarczyk 1991) in Błażowa in the exposure on the southwestern slope of Wielka Góra. During reconnaisance in other exposures, a single specimen (Text-fig. 43B) of a species unknown in Poland was found by Radosław Wasiluk M.Sc. at Krępak.

Amphipods occur in Błażowa. A single specimen was found in exposure B_4 by A. Jerzmańska in 1983 (Prof. K. Jażdżewski, pers. comm. 2006). Another specimen (Text-fig. 43E) was found by Mr. Rafał Nawrot in the exposure (described as B_1 by Kotlarczyk *et al.* 2006) a few tens of metres south of the collecting site of the material included in the present report. Two undescribed specimens (Text-fig. 43C–F) occurred at the locality Babice-Połanki.

Dragonflies occur at the locality Rudawka Rymanowska (layer 32), represented by a single, nearly complete specimen, albeit lacking one wing (Text-fig. 42A).

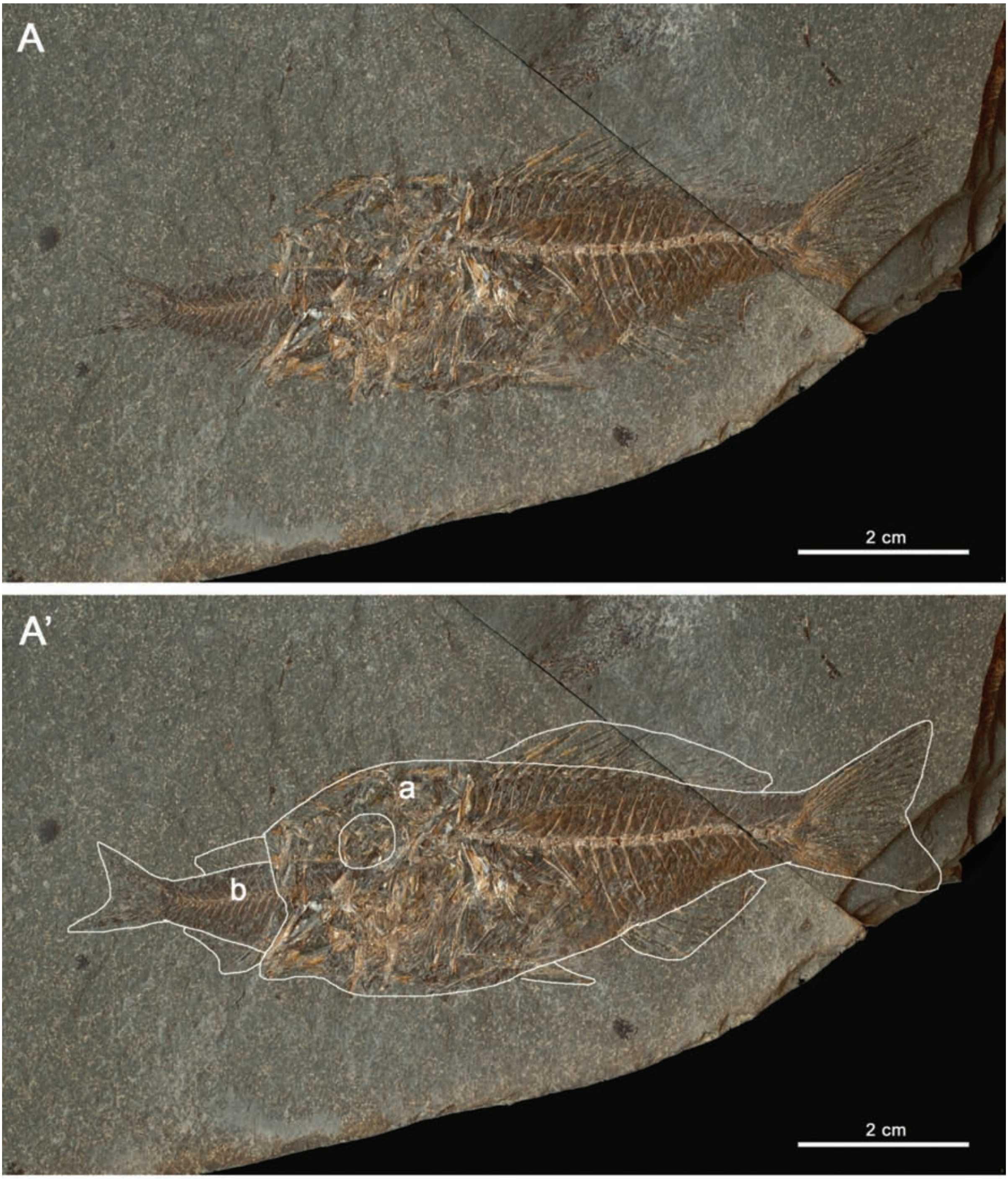
Bird remains occur at Jamna Dolna 1. A single specimen of a feather (Text-fig. 41A) was found by Dr. Wojciech Kozłowski over ten years ago, in the upper part of the exposure in units G and H. Of the two specimens collected in 2003–2006, one (Text-fig. 41C) was found by Dr. Piotr Zawrzykraj approximately at the boundary between units G and H. Another specimen (Text-fig. 41B) was found by Mrs. Iwona Dembicz in scree.

DISCUSSION AND COMPARISONS

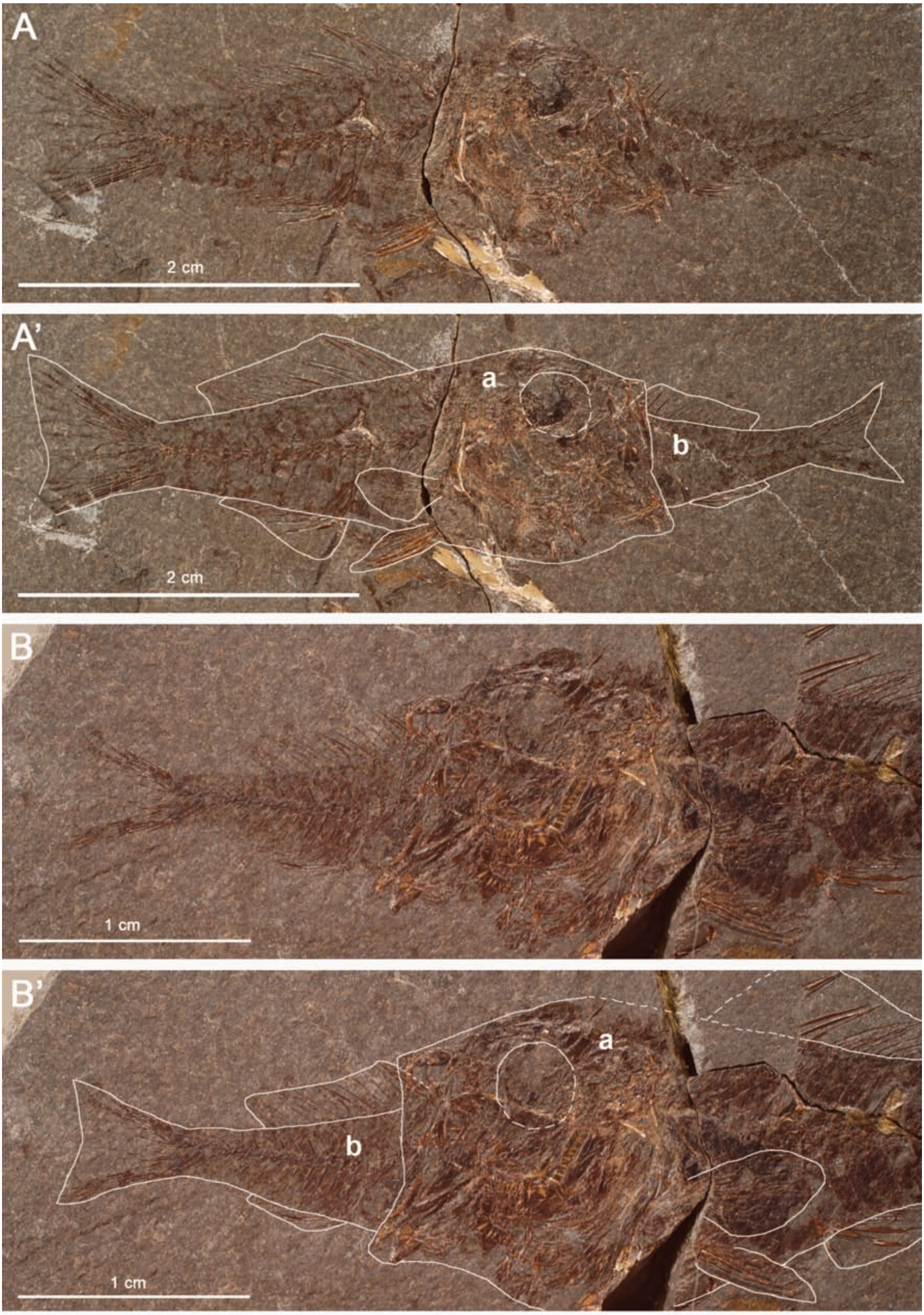
Interpretation of taphonomy

Articulated fish skeletons: The preservation of articulated fish skeletons indicates their entombment under quiet and very specific conditions (see further interpretations) prevailing at the burial place.

Disarticulated fish skeletons: Disarticulated skeletal elements detached from a fish carcass, lying commonly near the articulated portion of the skeleton (state A and type 1), indicate disarticulation as a result of decay of soft tissues at the burial place in a quiet environment (see Schäfer 1972). In rare cases, the state of preservation of specimens suggests the activity of macroscavengers or the action of bottom currents (Text-figs 24C, 25A, B; 40). In such cases, some skeletal elements are absent and/or widely separated from the articulated portion of the skeleton. Sometimes, disarticulated and displaced skeletal elements are

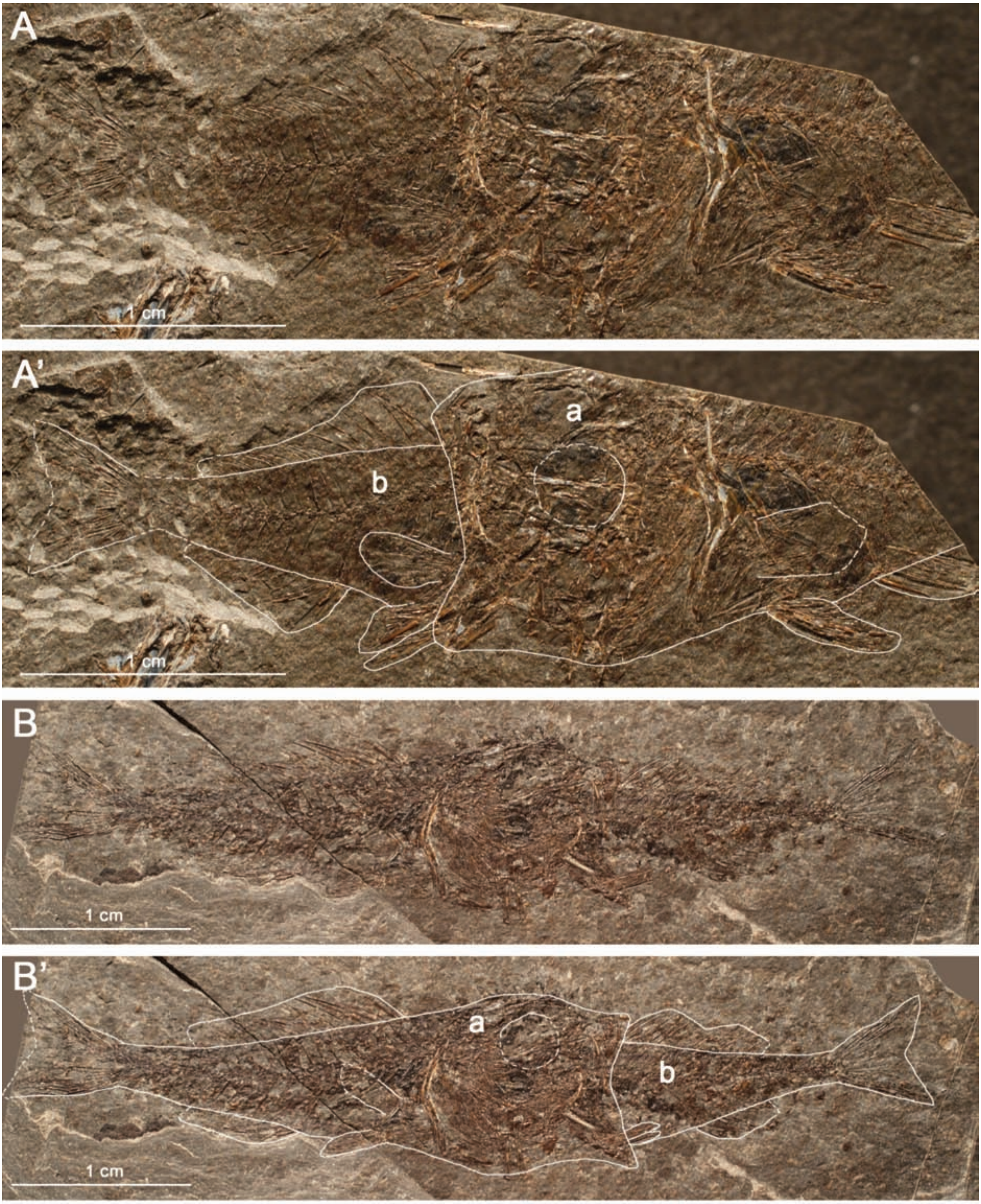


Text-fig. 32. Specimen of the family Serranidae that has choked to death on a smaller specimen of the same family (A,A'), locality Rudawka Rymanowska (layer 34), a – Specimen No. RU03.34.99, b – Specimen No. RU03.34.100



Text-fig. 33. Specimen of the family Serranidae that has choked to death on a smaller specimen of the same family, locality Rudawka Rymanowska (layer 34). **A**,**A'** – General view; **B**,**B'** – Close-up of the specimens, **a** – Specimen No. RU03.34.68, **b** – Specimen No. RU03.34.69

arranged in a unimodal direction, which may indicate the action of bottom currents. The states of preservation indicative of scavenging by macrobenthos, such as figured by Elder and Smith (1988, fig. 3), Wilson (1988, fig. 10A) and Ferber and Wells (1995, fig. 7B), seem to be totally absent.

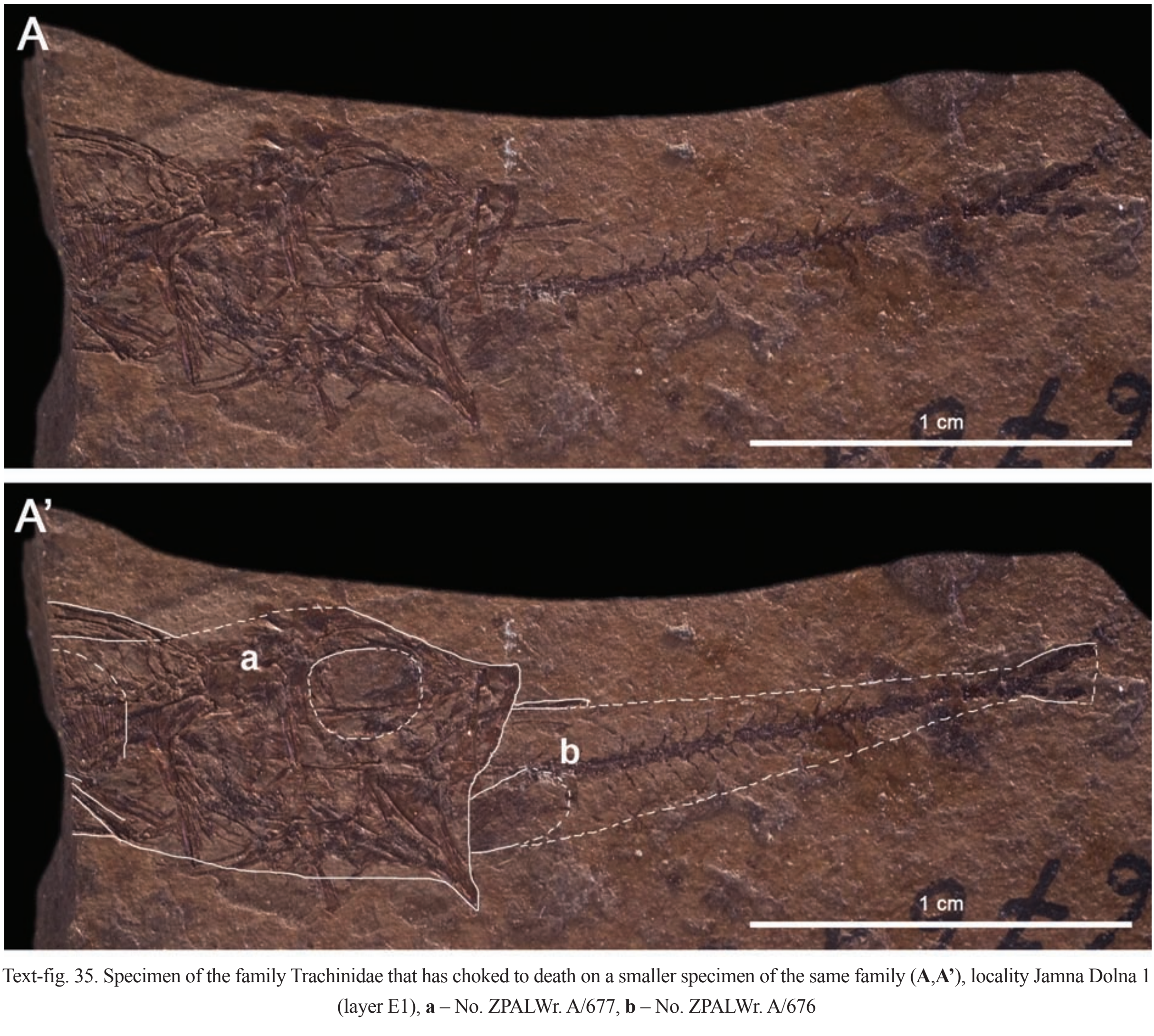


Text-fig. 34. Specimens of the family Serranidae that have choked to death on a smaller specimen of the same family, locality Rudawka Rymanowska. **A**,**A'** – Specimens from layer 32, **a** – No. RU01.32.58, **b** – No. RU01.32.59; **B**,**B'** – Specimens from layer WAP1, **a** – No. RU03.WAP1.47, **b** – No. RU03.WAP1.48

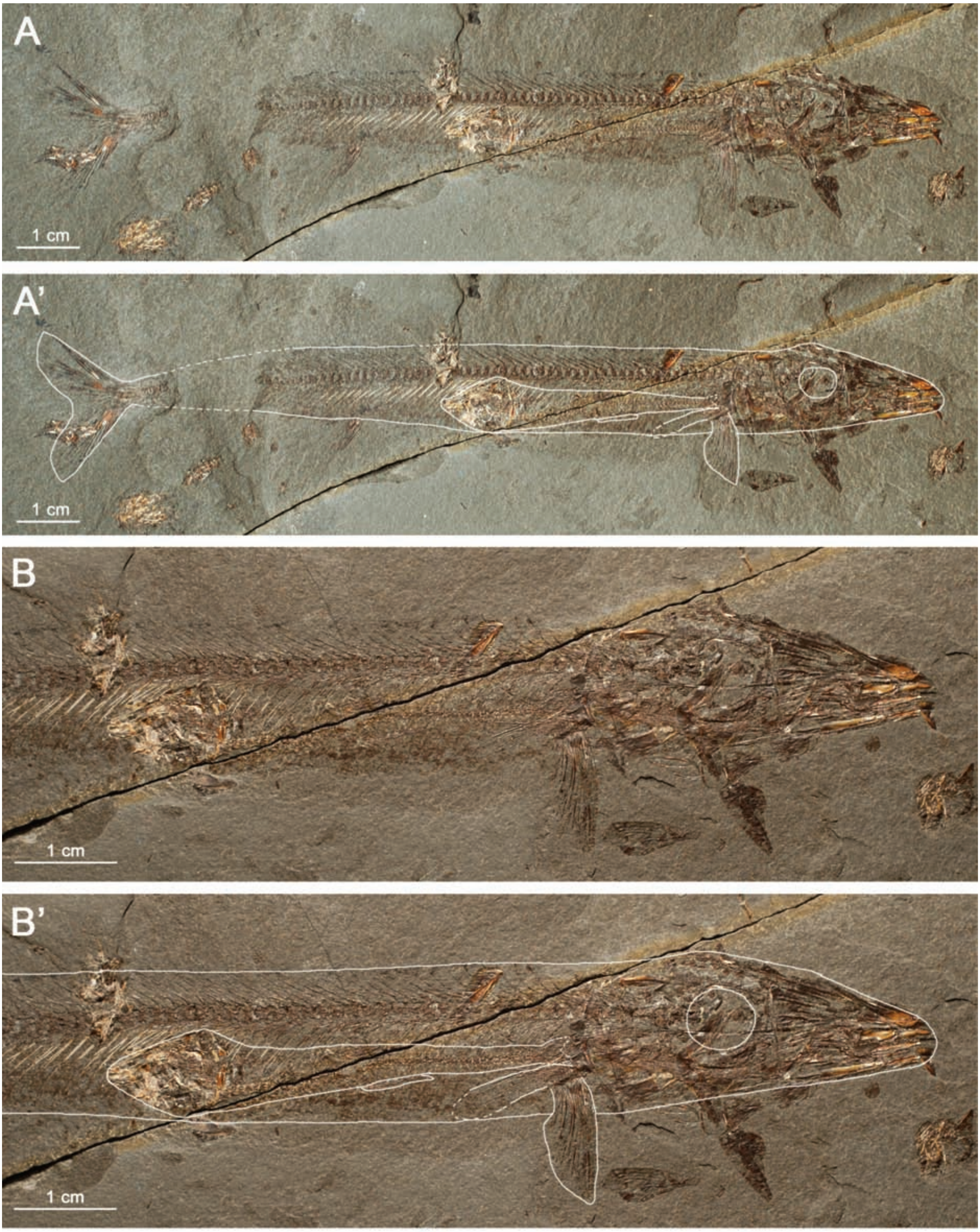
Some cases cannot be interpreted unequivocally. The state of preservation of specimens missing some skeletal elements, but surrounded by others (state B and type 1) may result either from a loss of skeletal elements in consequence of the decay of soft tissues during sinking before settling to the burial place, or from scavenging, or from the action of bottom currents (winnowing). The preservation of specimens displaying a portion of an articulated skeleton, but missing most or all skeletal elements of the remaining portion of the skeleton (state C), may result from feasts of predators, winnowing of disarticulated skeletal elements by bottom currents, or smashing of the fish body as a result of decay and bending. Disintegration of a carcass into two pieces as a result of decay and bending was noted in Recent fish of the family Clupeidae by Weiler (1929). A similar situation is recognized in the present study in a single specimen of this family (Text-fig. 24C).

Spatial arrangement of fish skeletons: Random orientation of the long axis of skeletons on bedding planes suggests generally a vertical settling of carcasses at the burial place.

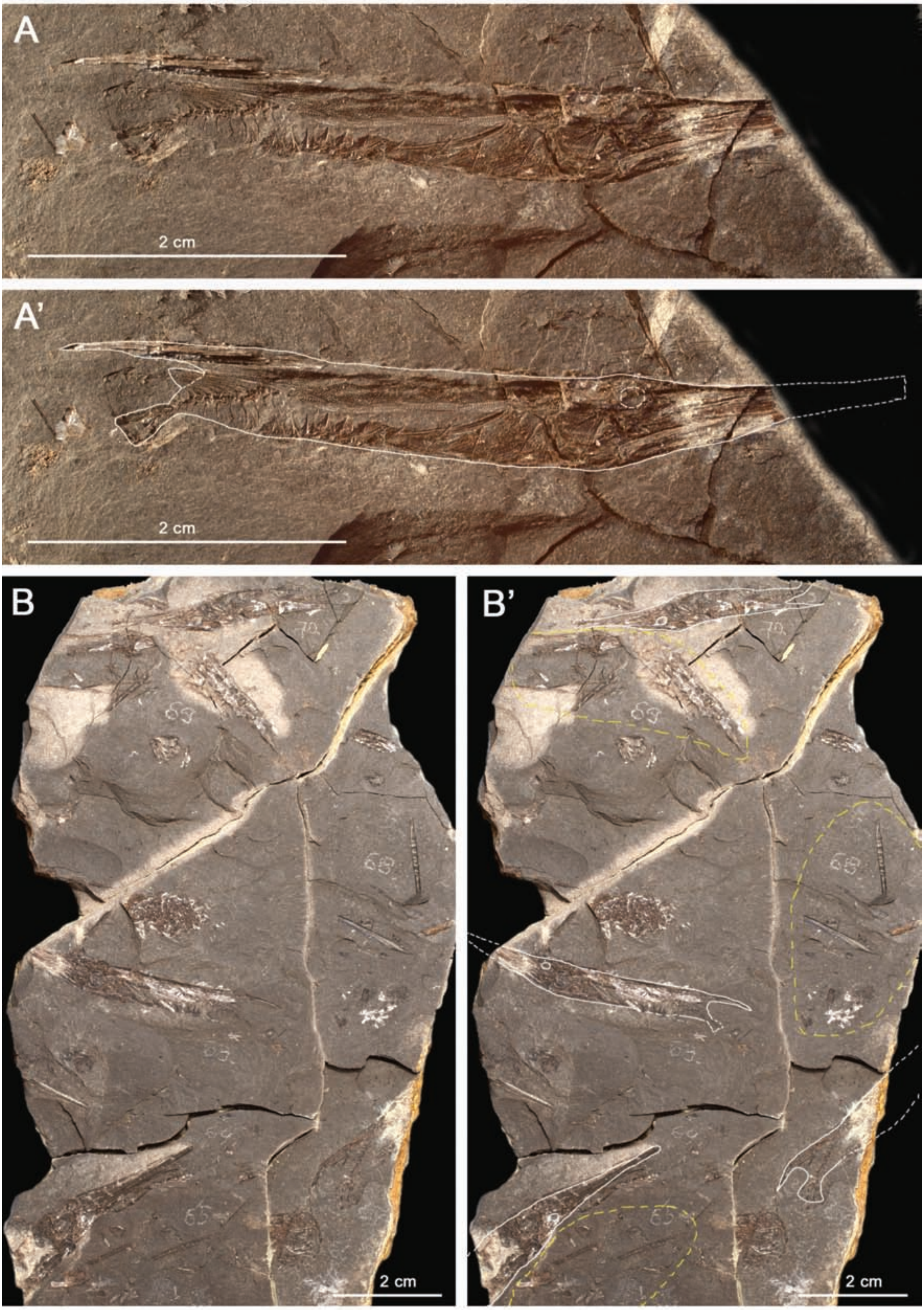
State of preservation of vertebral column, fins and jaws: A significant correlation between the taxonomic assignment of the fish and the state of preservation of its vertebral column reflects the influence of anatomy of the skeleton on its *post-mortem* deformation. The state of preservation of the vertebral column of representatives of the families Sternoptychidae, Myctophidae and Gonostomatidae is comparable to that observed by Jerzmańska (1960). The state of preservation of rare specimens (from ichthyotaphocoenoses JD1.E, JD1.E1 and WO), having the vertebral column deformed and the caudal fin detached and displaced, suggests that the vertebral column was deformed *post-mortem* at the burial place. It might have been caused either by the action



Text-fig. 35. Specimen of the family Trachinidae that has choked to death on a smaller specimen of the same family (**A**,**A'**), locality Jamna Dolna 1 (layer E1), **a** – No. ZPALWr. A/677, **b** – No. ZPALWr. A/676 of weak bottom currents, or by contortions due to dehydration. The vertebral column was presumably deformed when the carcass lay in a horizontal position at the bottom, as indicated by the position of the caudal fin (see Text-fig. 30). A comparably preserved specimen (see Hecker and Merklin 1946, pl. 2, fig. 2) of *Clupe-*



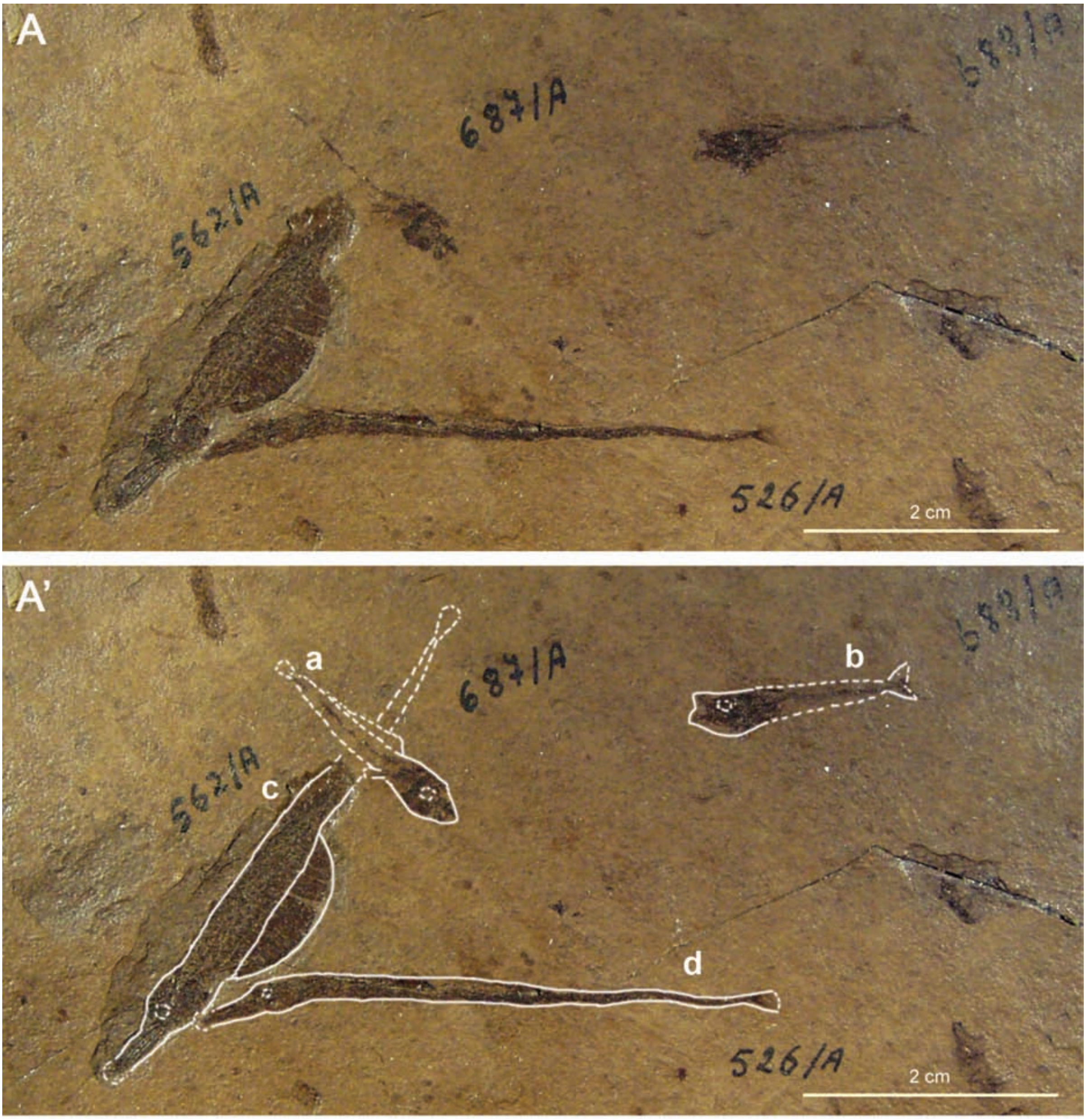
Text-fig. 36. Specimen of the species *Holosteus mariae* (Menner, 1948) with swallowed prey specimen of the family Argentinidae, locality Rudawka Rymanowska (layer 34). **A**,**A'** – General view, specimen No. RU03.34.101; **B**,**B'** – Close-up of the specimen



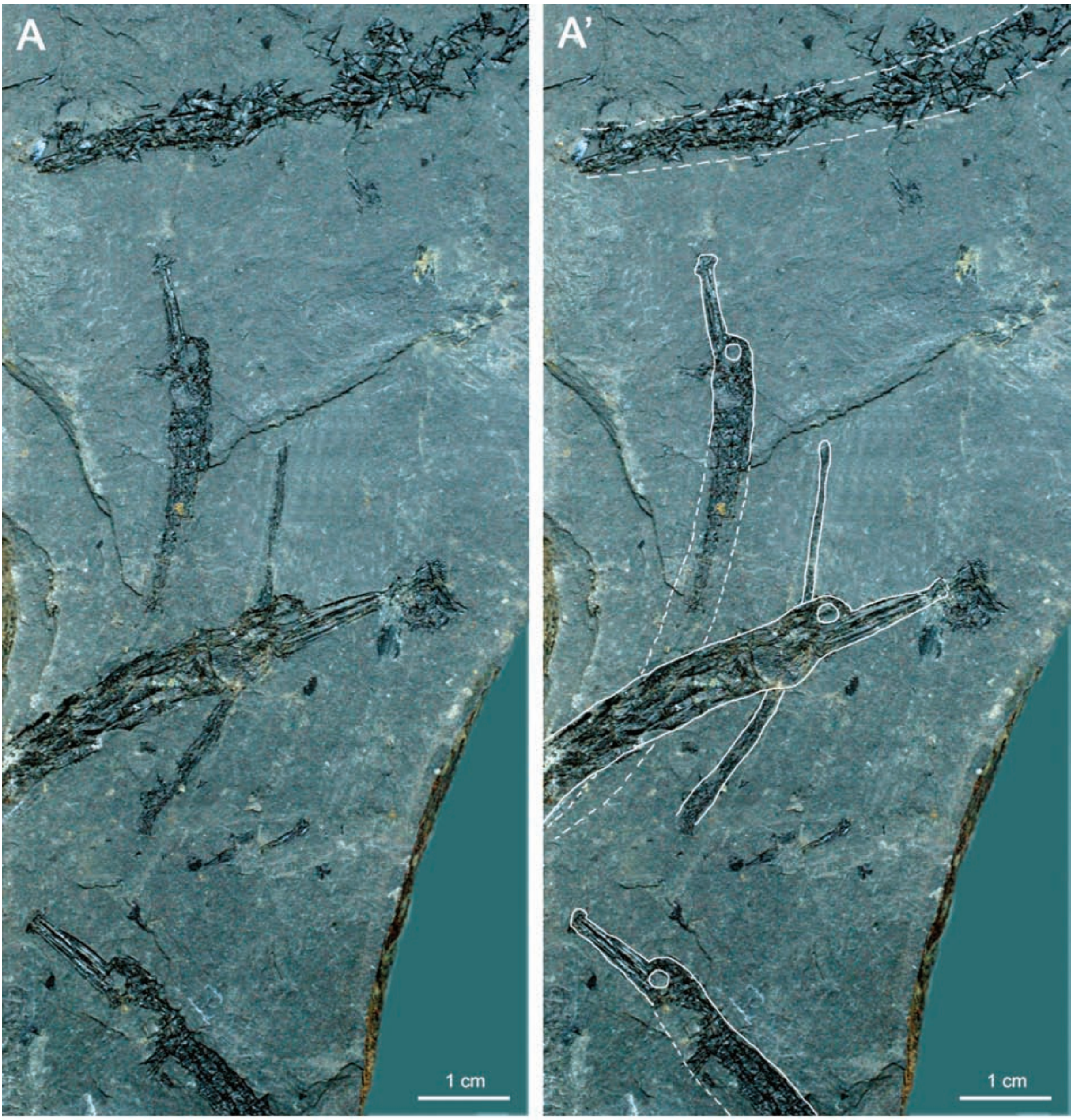
Text-fig. 37. **A**,**A'** – *Centriscus* sp., a representative of the family Centriscidae, Wujskie (layer 1) specimen No. WU.1.63; **B**,**B'** – Slab of Menilite Shale, to show the high density of individuals of the family Centriscidae in layer 1 at Wujskie, three of seven individuals are almost completely disarticulated (yellow-dashed outline), specimens No. WU.1.63 – WU.1.70

onella brevicauda (Menner, 1949) of the family Clupeidae from the Upper Maikop deposits of the Caucasus (Lower Miocene, according to Bannikov and Parin 1997) was interpreted by Hecker and Merklin (1946) as resulting from a weak current action, or from the decay and bloating of the carcass. A similarly preserved fish skeleton from the Solnhofen Limestone displays a *post-mortem* change from a slightly arched curvature to a stronger one, presumably due to dehydration in hypersaline bottom water (Seilacher et *al*. 1985, p. 12; pl. 1, fig. 7). From the Solnhofen Limestone, De Buisonjé (1972, fig. 2) illustrated a specimen of *Thrissops formosus* Agassiz that has the vertebral column arched and the caudal fin slightly displaced; in his interpretation, when the carcass changed position from vertical (with its front region above the bottom and caudal fin anchored in the sediment) to horizontal, the caudal fin was torn from the rest of the body.

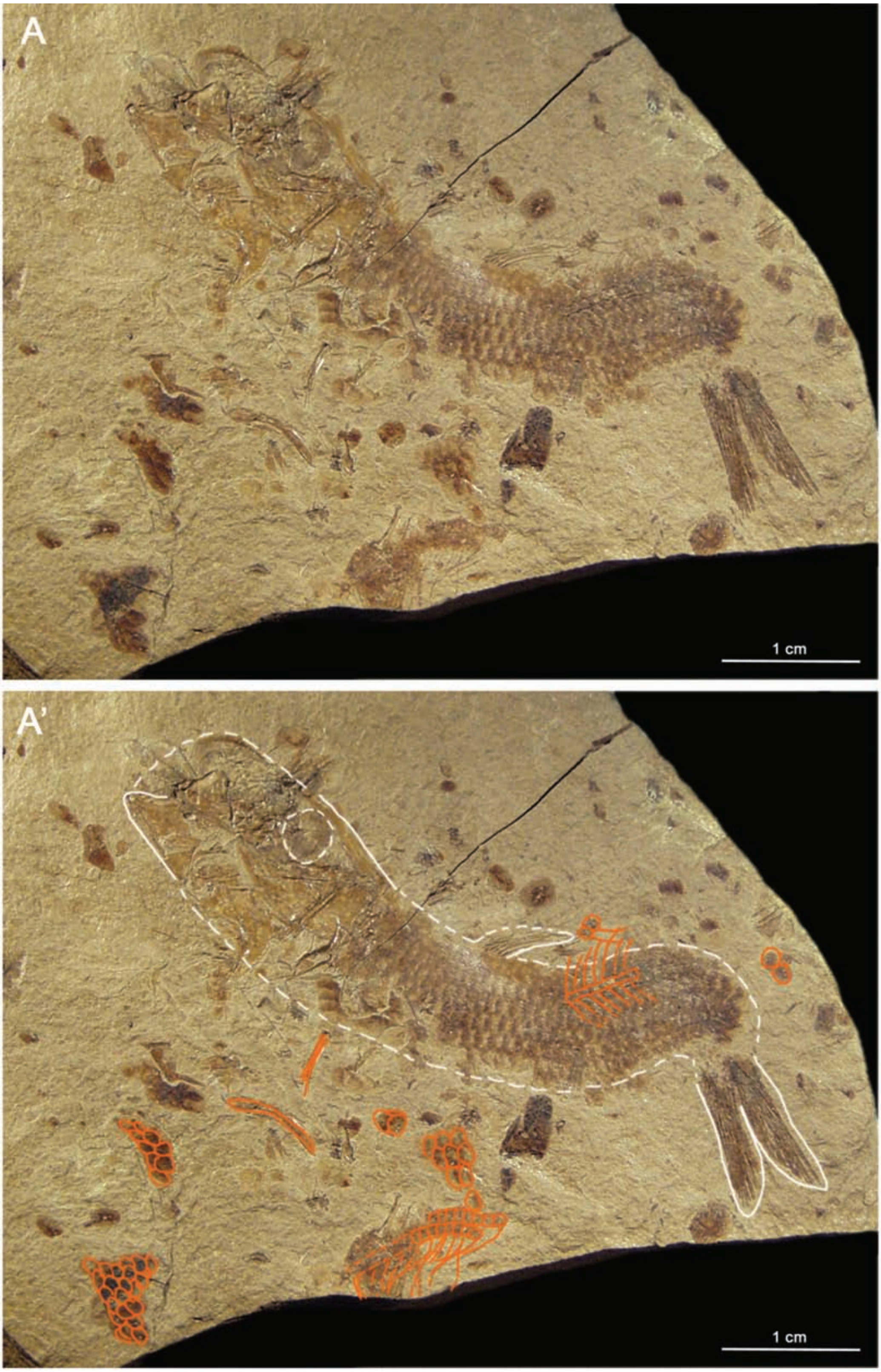
Some specimens with an arched vertebral column are articulated and show closed jaws. Such features speak against an interpretation that the vertebral column became arched due to extreme contraction of muscles



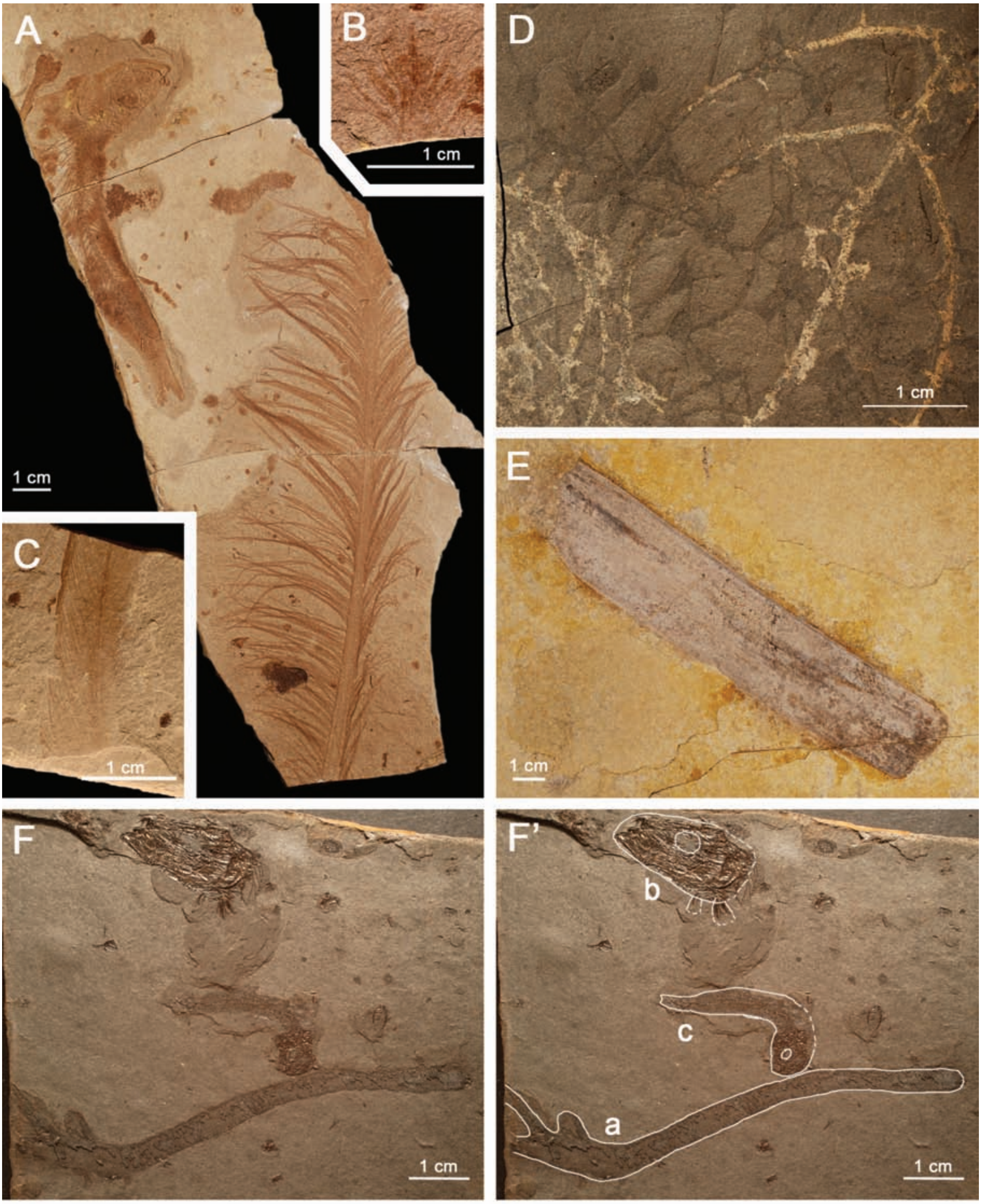
Text-fig. 38. **A**,**A'** – Slab of Menilite Shale, to show the high density of fish individuals in layer E1 at Jamna Dolna 1, **a** –*Trachinus minutus* (Jonet, 1958), specimen No. ZPALWr. A/687, **b** – *Trachinus minutus* (Jonet, 1958), specimen No. ZPALWr. A/688, **c** – *Hipposyngnathus neriticus* Jerzmańska, 1968, specimen No. ZPALWr. A/562, **d** – *Syngnathus* sp., specimen No. ZPALWr. A/526 during death caused by suffocation (see Paucă 1933; Gaudant 1989; Wilson 1988, 1996; Ferber and Wells 1995) or due to bloating and decay of the body (see Weiler 1929). However, neither natural *post-mortem* change (see Weiler 1929), weak bottom current action (see Hecker and Merklin 1946), dehydration (Seilacher *et al*. 1985; Maisey 1991; Ferber and Wells 1995) nor buoyancy of the abdominal portion filled with gas (Weiler 1929; Schäfer 1972; Maisey 1991) can be excluded as causing the arched and *S*-shaped curvatures of the specimens studied. Moreover, an arched curvature of the vertebral column may presumably result from hydraulic resistance of the carcass during settling to the burial place. Irregular curvature could be a result of a few factors (current action, dehydration, buoyancy), but it indicates that the decaying soft tissues were then distinctly weaker than during life and did not keep the shape of vertebral column (see Hecker and Merklin 1946). The specimen of the Argentinidae having its vertebral column curved irregularly (Text-fig. 29C), and many other specimens, give the impression that they were deformed just when settling to the bottom. This



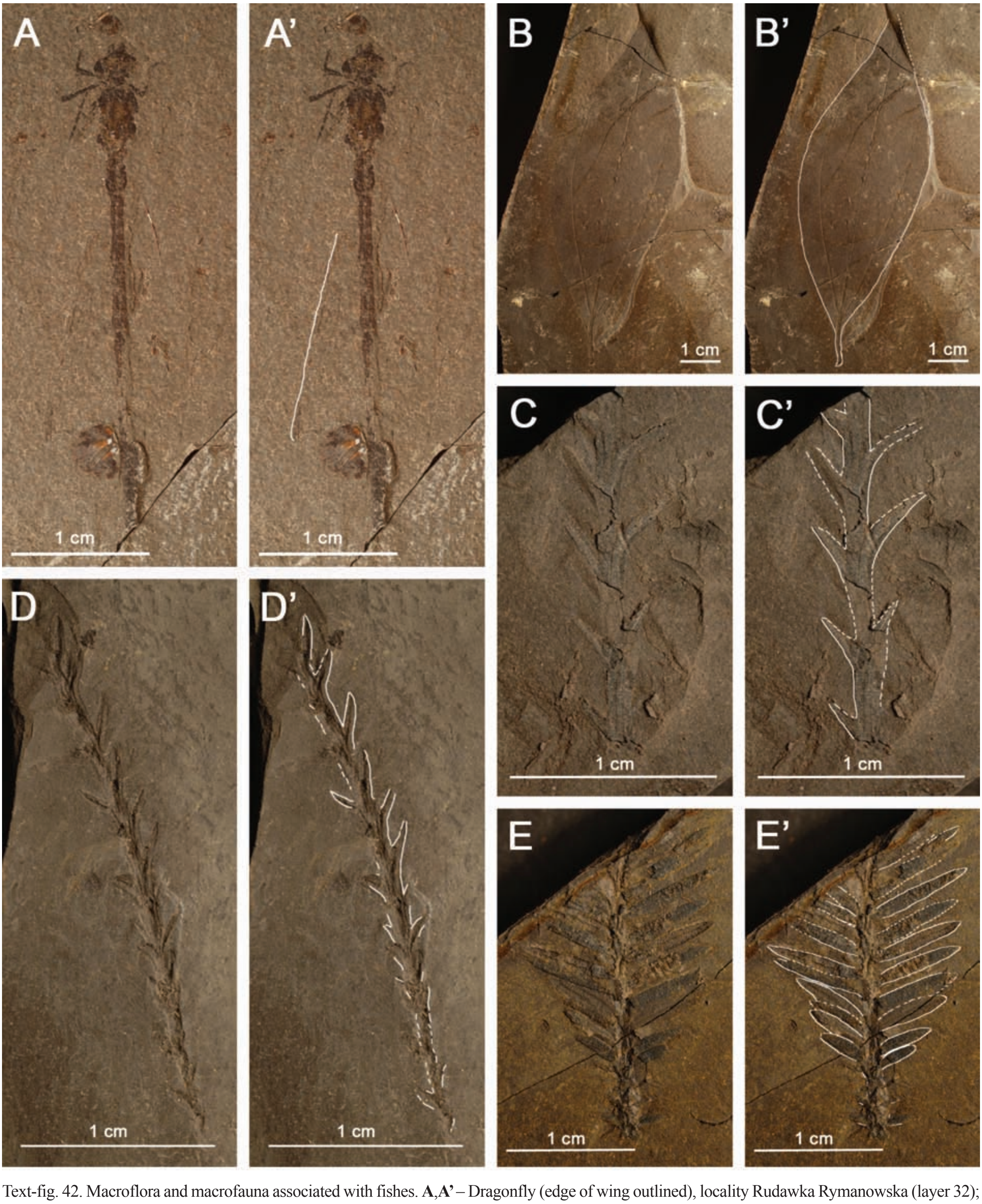
Text-fig. 39. **A**,**A'** –Slab of Menilite Shale, to show the high density of fish individuals in layer K at Jamna Dolna 2; specimens No. JD2.K.131 – JD2.K.135



Text-fig. 40. **A**,**A'** – Disarticulated skeleton of a specimen of the family Clupeidae, to show the spatial arrangement of its skeletal elements (some in orange outline), resulting presumably from the activity of macro-scavengers or bottom currents; locality Jamna Dolna 1 (unit E), specimen No. ZPALWr. A/322 also applies to specimens of the Argentinidae with their vertebral column curved in a circle (see Text-fig. 29A, B). The presence of mechanical agents is supported by the breakage of the vertebral column just posterior to the head (see Text-fig. 29A). Specimens with the vertebral column curved in a circle do not represent the gastric



Text-fig. 41. Macroflora and macrofauna associated with fishes. **A-C** – Bird feathers, locality Jamna Dolna 1: **A** – Feather and a fish of the family Clupeidae, unit G-H, specimen from private collection of Dr.Wojciech Kozłowski; **B** – Feather, collected by Mrs. Iwona Dembicz, private collection, specimen from the scree; **C** – Feather, collected by Dr. Piotr Zawrzykraj, private collection, unit G-H; **D** – Algae, locality Jamna Dolna 2 (scree); **E** – Fragment of wood, locality Wola Czudecka (unit WO); **F**,**F'** – Fragment of wood (**a**), near of a fish skull (**b**) and a well-preserved complete skeleton (**c**) of a fish of the family Clupeidae, locality Jamna Dolna 2 (layer Z) ejection of a larger predator, as was once suggested by Janicke (1970) for a slightly similar specimen of *Strobilodus* sp. from the Solnhofen Limestone. However, the influence of current action on an arched curvature should be assumed. In such a situation the weak bottom current moves tail to head. Such an influence was already suggested by Hecker and Merklin (1946; p. 654; fig. 1 II f, 2) for a specimen of *Clupeonella brevicauda* (Menner, 1949) of the family Clupeidae with its vertebral column curved in a circle.

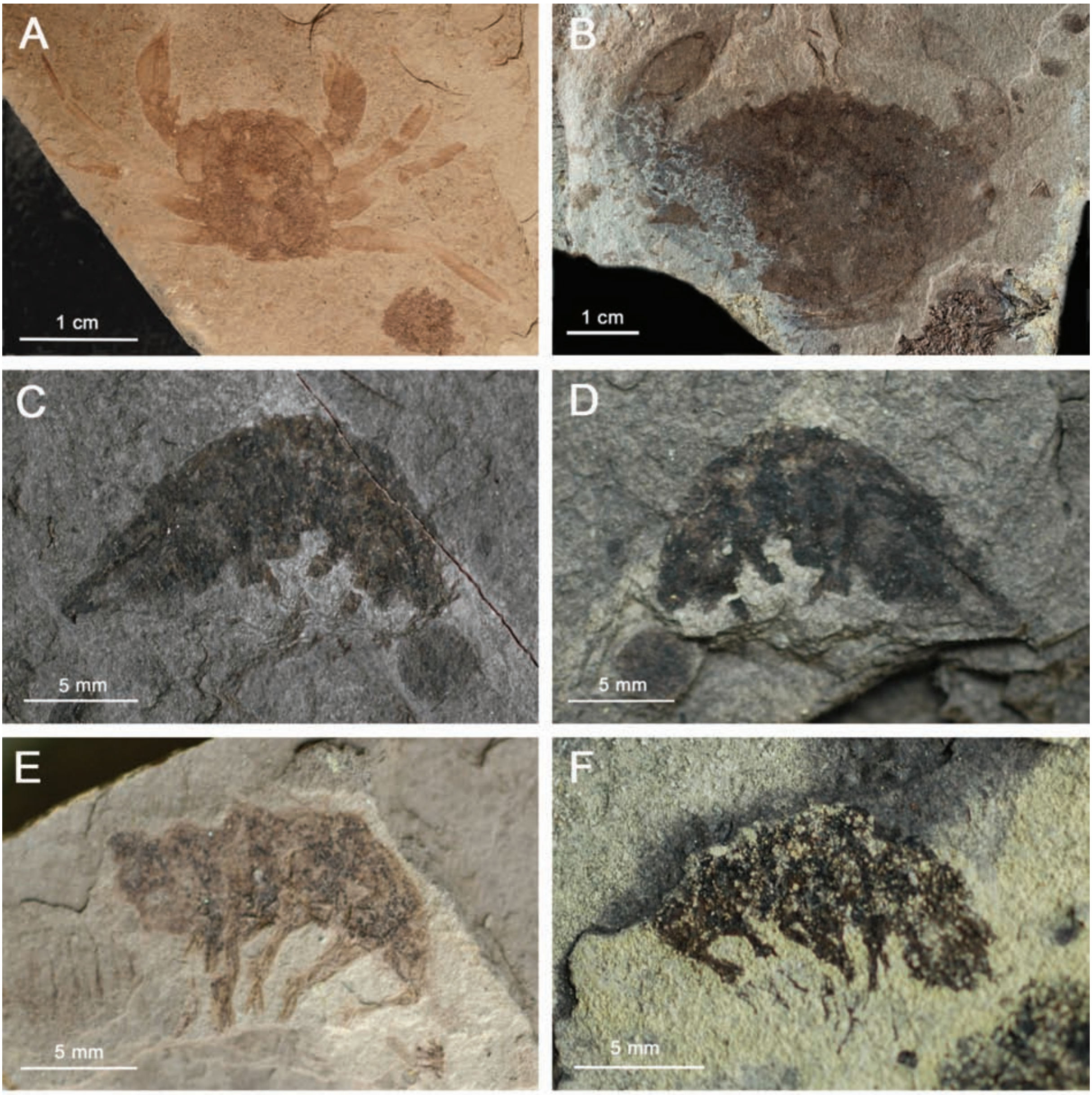


Text-fig. 42. Macroflora and macrofauna associated with fishes. **A**,**A'** – Dragonfly (edge of wing outlined), locality Rudawka Rymanowska (layer 32); **B**,**B'-E**,**E'** – terrestrial plant detritus, locality Jamna Dolna 2 (B-D from layer X, E from layer U)

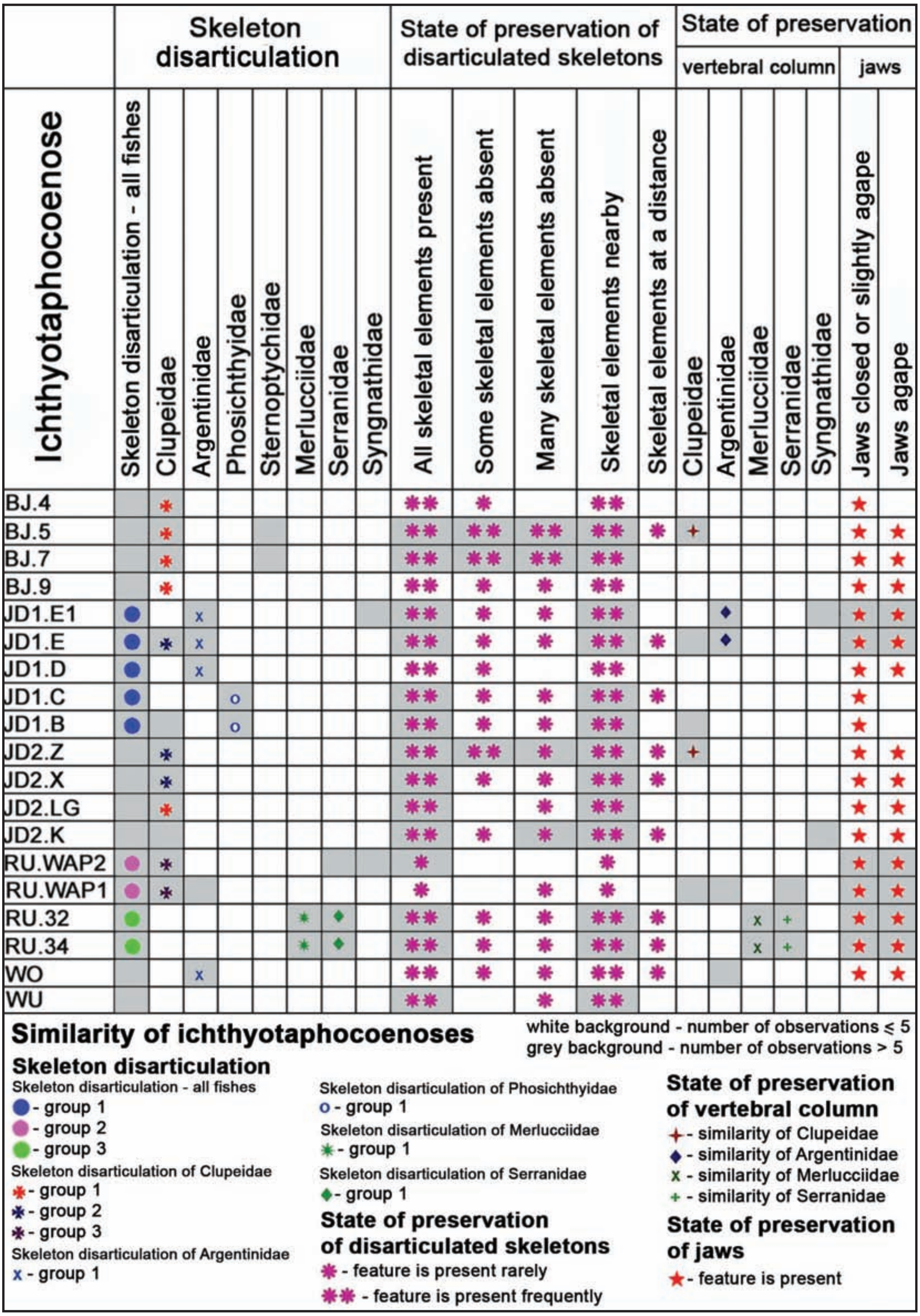
Jaws preserved either closed or agape are common in most of the ichthyotaphocoenoses studied. Jaws agape are common in examples of catastrophic death resulting from suffocation or poisoning (Paucă 1933; Elder and Smith 1988; Wilson 1988; Ferber and Wells 1995). The presence of jaws closed in many examples in the present study suggests that the death of the fishes may also be attributable to other factors (e.g. rapid change of water temperature; diseases due to bacteria, parasites, viruses, fungi). Thus, it should be considered that each ichthyotaphocoenose can contain individuals that died not only during a mass mortality event but also over periods of time.

The variability in preservation of fins is affected by bloating and decay of the carcass. A fin with erect rays may indicate a sudden death (see Wilson 1996) from suffocation or poisoning. Specimens displaying the jaws agape and all of the fins with erect rays probably died of suffocation or poisoning.

Unusual cases of preservation: Specimens of a fish which has choked to death on a smaller fish show a case



Text-fig. 43. Macrofauna associated with fishes. **A** – Crab, locality Jamna Dolna 1 (unit G or H); **B** – Crab, nearby locality Krępak, collected by Radosław Wasiluk M.Sc; **C-D** – Amphipod (part and counterpart), locality Babice-Połanki; **E** – Amphipod, locality Błażowa, collected by Mr. Rafał Nawrot; **F** – Amphipod, locality Babice-Połanki of predation. Specimens of the family Serranidae both in the Oligocene and nowadays (of the genera *Epinephelus, Mycteroperca, Cephalopholis*) may attack fishes of the same family; for instance, individuals of the present-day *Epinephelus striatus* (Bloch, 1792) are known to swallow smaller specimens of the same species (Froese and Pauly 2008). A case of cannibalism of the species *Serranus budensis* (Heckel, 1856) of the



	Skeleton disarticulation								State of preservation of disarticulated skeletons					State of preservation						
														vertebral column					jaws	
Ichthyotaphocoenose	Skeleton disarticulation - all fishes	Clupeidae	Argentinidae	Phosichthyidae	Sternoptychidae	Merlucciidae	Serranidae	Syngnathidae	All skeletal elements present	Some skeletal elements absent	Many skeletal elements absent	Skeletal elements nearby	Skeletal elements at a distance	Clupeidae	Argentinidae	Merlucciidae	Serranidae	Syngnathidae	Jaws closed or slightly agape	Jaws agape
BJ.4		✱							✱✱	✱		✱✱							★	
BJ.5		✱							✱✱	✱✱	✱✱	✱✱	✱	+					★	★
BJ.7		✱							✱✱	✱✱	✱✱	✱✱							★	★
BJ.9		✱							✱✱	✱	✱	✱✱							★	★
JD1.E1	🔵		x						✱✱	✱	✱	✱✱			◆				★	★
JD1.E	🔵	✱	x						✱✱	✱	✱	✱✱	✱		◆				★	★
JD1.D	🔵		x						✱✱	✱		✱✱							★	★
JD1.C	🔵			o					✱✱	✱	✱	✱✱	✱						★	
JD1.B	🔵			o					✱✱	✱	✱	✱✱							★	
JD2.Z		✱							✱✱	✱✱	✱	✱✱	✱	+					★	★
JD2.X		✱							✱✱	✱	✱	✱✱	✱						★	★
JD2.LG		✱							✱✱		✱	✱✱							★	★
JD2.K									✱✱	✱	✱	✱✱	✱						★	★
RU.WAP2	🟣	✱							✱			✱							★	★
RU.WAP1	🟣	✱							✱		✱	✱							★	★
RU.32	🟢					✱	◆		✱✱	✱	✱	✱✱	✱			x	+		★	★
RU.34	🟢					✱	◆		✱✱	✱	✱	✱✱	✱			x	+		★	★
WO			x						✱✱	✱	✱	✱✱	✱						★	★
WU									✱✱		✱	✱✱								

Similarity of ichthyotaphocoenoses

white background - number of observations ≤ 5
grey background - number of observations > 5

Skeleton disarticulation

Skeleton disarticulation - all fishes
🔵 - group 1
🟣 - group 2
🟢 - group 3

Skeleton disarticulation of Clupeidae
✱ - group 1
✱ - group 2
✱ - group 3

Skeleton disarticulation of Argentinidae
x - group 1

Skeleton disarticulation of Phosichthyidae
o - group 1

Skeleton disarticulation of Merlucciidae
✱ - group 1

Skeleton disarticulation of Serranidae
◆ - group 1

State of preservation of disarticulated skeletons
✱ - feature is present rarely
✱✱ - feature is present frequently

State of preservation of vertebral column
+ - similarity of Clupeidae
◆ - similarity of Argentinidae
x - similarity of Merlucciidae
+ - similarity of Serranidae

State of preservation of jaws
★ - feature is present

Text-fig. 44. Comparison of ichthyotaphocoenoses from Oligocene of the Outer Carpathians of Poland same family was recorded in the Oligocene Menilite Shales from Romania (Paucă 1932, 1933) and in the Oligocene marls with *Meletta* (French, *Marnes à Mélettes*) at the Froidefontaine locality (southern Rhine Graben) in France (Pharisat 1991). The presumed prey became stuck in the mouth of the predator, and the fin spines did not allow it to escape. This prey individual may well have been toxic (poisonous) for the predator, because individuals of the Serranidae can have venomous spines, or can periodically contain toxin in skin and muscles (Froese and Pauly 2008). Pharisat (1991) interpreted such a state of preservation as a vomit of the predator during traumatic death. Evidence of cannibalism (see Text-fig. 35) of *Trachinus minutus* (Jonet, 1958) of the family Trachinidae is herein recorded for the first time in the fossil state. The prey individual either became stuck in the mouth of the predator by its fin spines, or it was venomous. Note that most recent species of the Trachinidae are venomous for people (Froese and Pauly 2008).

Other evidence of predation is displayed by specimens of a fish containing a prey fish individual in its stomach (fish with a swallowed prey fish). The predator may have died because of the poison of the prey rather than from senility or disease; a diseased individual usually does not eat just before its death, especially if it must hunt its prey in a longer spurt (see Viohl 1990). Specimens of *Holosteus mariae* (Menner, 1948) of the family Paralepididae record predation on individuals of the families Serranidae (Bieńkowska 2002, fig. 43 = 2004b, fig. 20), Myctophidae ("*Diaphus*" *moravicus*; Prokofiev 2005b, pp. 297 and 300, fig. 1c) and Argentinidae (see Text-fig. 36).

Comparison of the ichthyotaphocoenoses

Analysis of the three taphonomic features: degree of skeleton disarticulation; state of preservation of disarticulated skeletons, state of preservation of vertebral column (e.g. straight, curved, broken), fins, and jaws, reveals the similarity between ichthyotaphocoenoses JD1.E and JD1.E1, between RU.34 and RU.32, and between RU.WAP1 and RU.WAP2 (see Text-fig. 44). The peculiarity in taxonomic composition of ichthyotaphocoenose WU.1 in relation to the other ichthyotaphocoenoses precludes recognition of any taphonomic similarity. The limited number of taphonomic observations in otaphocoenoses BJ.4, BJ.9, JD1.D and WO permits only the observation that there is some very slight similarity to the other ichthyotaphocoenoses.

Some features are similar in most of the ichthyotaphocoenoses. Firstly, the skeletons are commonly in different stages of skeleton disarticulation (see Text-figs 17–20), and each ichthyotaphocoenose contains not less than three stages of skeleton disarticulation. Secondly, most of the ichthyotaphocoenoses (16 out of 19) contain a high percentage of individuals that are more or less disarticulated, while articulated specimens constitute less than 40% of the total. Thirdly, usually disarticulated skeletal elements remain near the articulated portion of the skeleton. Moreover, jaws preserved both closed and agape are common in most of the ichthyotaphocoenoses (Text-fig. 44).

All of the ichthyotaphocoenoses were compared in order to recognize if the lithology of the fish-bearing layer influences the state of preservation of the fishes. The strong similarity between ichthyotaphocoenoses RU.WAP1 and RU.WAP2, from the Tylawa Limestones, and dissimilarity of both of them to the remaining ones indicates the influence of lithology on the state of fish preservation. Such correlation is also distinct in the case of ichthyotaphocoenoses RU.34 and RU.32, both from dark grey calcareous shales. On the other hand, the ichthyotaphocoenoses from black shales, BJ.5, BJ.7, JD2.K, JD2.LG, JD2.Z and JD2.X, are more or less different from one another; for instance, a high percentage of disarticulated skeletons devoid of many skeletal elements (State C) distinguishes ichthyotaphocoenose BJ.5 from JD2.Z.

Sedimentologic interpretation of the fish-bearing deposits

All dark-coloured shales of platy fissility or laminated: All these dark-coloured shales are a product of a low sedimentation rate, that is, of slow accumulation in calm waters (see also Jerzmańska and Kotlarczyk 1968, p. 56; Kotlarczyk *et al.* 2006, p. 25), as is indicated by their clay-sized particles and irregular parallel lamination indicated by variability of colour.

The constituent particles of the shales were presumably deposited under the influence of anoxic bottom waters, as indicated by lamination, dark colour, and presence of fish skeletons. Subtle differences in the colour (grey/black) of the laminae in grey and black laminated shales indicate periodic changes in the redox state.

The average sedimentation rate for such shales was estimated as 1cm/10^3 years (Kotlarczyk 1988). The thickness of the fish-bearing layers BJ.9, BJ.7, BJ.5, BJ.4, JD1.E1, RU.34, RU.32, JD2.K, JD2.LG, JD2.Z, JD2.X and WU.1 ranges from 1 to 10 cm, and thus, each of these layers records a period of a few thousand years. The fish-bearing units JD1.B, JD1.C, JD1.D and JD1.E are a few metres thick, and record much longer periods of time.

Laminated limestones: Parallel lamination, comprising light coloured laminae composed of calcite micrite, and darker laminae, enriched in organic matter and clay minerals), indicates periodic changes of conditions, and the accumulation of calcareous ooze and phytoplankton by vertical settling (Jucha and Kotlarczyk 1961, Koszarski and Żytko 1961; Nowak 1965; Jucha 1969; Haczewski 1989; see also Pickering *et al*. 1986). Bright laminae resulted from long-lasting and intense blooms of coccolithophores (Haczewski 1989). The sedimentation rate for these laminated limestones was estimated as low (Jucha and Kotlarczyk 1961; Koszarski and Żytko 1961; Nowak 1965; Jucha 1969; Haczewski 1989), as about a few millimetres in a thousand years (Kotlarczyk *et al*. 2006, pp. 25, 38).

The fish-bearing layers WAP1 and WAP2 from Rudawka Rymanowska, 3 cm and 15 cm, respectively, record a period from a few to more than ten thousand years of pelagic sedimentation.

Marls: Marl laminae are presumably a result of pelagic sedimentation and/or deposition from low-concentration turbidity currents (see Pickering *et al*. 1986).

The origin of the marl unit (Dynów Marls Member) has not been clearly explained yet. It is supposed to have originated as a result of the activity of submarine fans, the activity of bottom currents directed SSE, in some cases by olistostromes, and/or deposition from low-concentration turbidity currents (Kotlarczyk 1985, 1991; Kotlarczyk and Leśniak 1990; Kotlarczyk *et al*. 2006), or blooms of coccolithophores (Krhovský 1981). Sedimentation rates of these marls are more or less similar to that of one of the shales of the Menilite Formation, estimated as 1 cm/ 10^3 years (see Kotlarczyk 1988).

The fish-bearing layers at Wola Czudecka occur as marl laminae interbedding beds of marls. The presence of fish scales or plant detritus allows recognition of normal grading in some beds, indicating deposition from turbidity currents. Unit WO, 15 m thick, consisting mainly of marls, records a longer period of sedimentation with variable rates (from low to high), of about a few hundred thousand years.

Normally graded sand-shale couplets: Commonly, there occur couplets comprising basal sandstones with ripple-drift lamination that grade up into shales of leaf-like fissility. They are deposits of low concentration turbidity currents, as is indicated by the presence of thin beds, a high shale/sandstone ratio, normal grading of fish skeletal elements and mineral grains (see Pickering *et al*. 1986).

Non-laminated shales of leaf-like fissility: The normal grading of fish scales indicates deposition from low concentration turbidity currents.

Origin of the ichthyotaphocoenoses

Jerzmańska and Kotlarczyk (1968) interpreted the ichthyotaphocoenoses from locality Jamna Dolna 1 as resulting from the settling of carcasses under quiet bottom conditions and a low sedimentation rate, but they did not exclude some transport of the fishes. The cause of death of the fishes remained open to question. Recently, Kotlarczyk *et al*. (2006) assumed that many fishes were transported from their life environment to the bottom of a more than 2,000 m deep basin. This concerned the fishes assigned in the paleoecological analysis to neritic and littoral waters or occurring at, or close to, the bottom of continental slopes or submarine ridges and mounts. According to the paleoecological classification of Kotlarczyk *et al*. (2006, pp. 71–79) such life habitats were typical of representatives of the Merlucciidae, Zeidae, Caproidae, Syngnathidae, Centriscidae, Serranidae, Priacanthidae, Ammodytidae, Trachinidae, Gempylidae, and Trichiuridae.

Ichthyotaphocoenose WU.1, which records the so-called *2nd Centriscus* Event, was interpreted by Kotlarczyk *et al*. (2006) as resulting from a mass mortality. The origins of the other fish-bearing layers in the Outer Carpathians of Poland were considered to be attributable to different factors (Jerzmańska and Kotlarczyk 1968, Kotlarczyk *et al*. 2006), albeit ones that are not readily identifiable. It was suggested (Kotlarczyk and Jerzmańska 1988, Kotlarczyk *et al*. 2006) that articulated skeletons are preserved either due to a quiet environment, pelagic sedimentation, anoxic conditions in the sediment and presumably in the bottom waters, or to sinking into soft sediment.

Causes of death of the fishes

The causes of death of fishes may include (see Schäfer 1972; Elder and Smith 1988) diseases caused by viruses, bacteria, fungi, parasites; or a rapid change of temperature or chemistry of the environment (e.g. heat shock, anoxia, alkaline shock, saline shock, toxicity). A catastrophic mass mortality may be caused by sudden massive reproduction (blooms) of dinoflagellates, diatoms, or coccolithophores. When dinoflagellates or diatoms occur in large quantities the water colour changes – what is commonly called the ‘red tide’. Some dinoflagellates produce toxins and the sea water then changes chemically, causing the death of the fish population. Some diatoms have long thin spines on their frustules, which may cause gill disease and death by suffocation. A similar effect can be caused by the presence of suspended matter in water for a long period. The decomposition of mass quantities of plankton leads to a considerable decrease in oxygen content, which can also cause suffocation. Abiotic factors, such as volcanic eruption or tsunami, may also contribute to a mass mortality of fishes.

Features such as a high density of individuals, a predominance of fishes displaying jaws agape and fins with rays erect, and a high percentage of juvenile individuals (see Paucă 1933; McGrew 1975; Elder and Smith 1988; Wilson 1988, 1996) may indicate a catastrophic mass mortality, which is typical of a thanatocoenose. None of the ichthyotaphocoenoses studied displays a significant predominance of fishes having jaws agape and erect rays. In ichthyotaphocoenoses JD2.K and WU.1 these features are not indicative, because of the predominance of such peculiar fishes as the Syngnathidae in JD2.K (Text-fig. 32C), and the Centriscidae in WU.1 (Text-fig. 41A). There is a high density of individuals in the fish-bearing layers yielding ichthyotaphocoenoses JD1.E1, JD2.K, and WU.1, and a high percentage of juvenile individuals in ichthyotaphocoenoses JD1.E1 (Jerzmańska and Kotlarczyk 1968) and JD2.Z. Thus, each of the ichthyotaphocoenoses displays some features indicative of a mass mortality, but none of them has a set of features indicating it unequivocally. Therefore, the cause and/or conditions of death were not the same for all individuals. Presumably, only some individuals died instantaneously during mass mortalities, whereas the majority died instead over a period of time as a result of senility, diseases, or other circumstances.

Post-mortem history until settling at burial place

Soft tissues begin to decompose soon after death and, after just a few days or even hours, in oxidized water, significant signs of decomposition are visible (see Weiler 1929, Schäfer 1972). An articulated skeleton can be preserved (fossilized) only if it reaches the burial place soon after death (Schäfer 1972). Such an opinion, accepted by Jerzmańska and Kotlarczyk (1968, 1973), is applicable to the ichthyotaphocoenoses studied here. The majority of fishes of the Menilite-Krosno Series are represented by forms that did not live close to the bottom. Therefore, for most or all of the fishes studied it should be assumed that the burial place was at a distance from the place of death. Jerzmańska and Kotlarczyk (1968, 1973) inferred that fish carcasses sank to the burial place without transport by currents, but probably with a slight displacement. On the other hand, according to Kotlarczyk *et al.* (2006), the presence of littoral fishes together with bathypelagic ones in a single ecostratigraphic zone is caused by a *post-mortem* transport from shallow water to deep water. Probably the majority of the fishes lived in the water column above the depositional site. Only some fishes were probably more or less transported horizontally. For example, such horizontal transport must be assumed for littoral fishes (Trachinidae) in the ichthyotaphocoenoses from Jamna Dolna 1 that also contain bathypelagic fishes (e.g. Gonostomatidae, Phosichthyidae). Remains of terrestrial biota occur in many of the fish-bearing layers. They are represented by bird feathers at Jamna Dolna 1, dragonflies (single specimen) at Rudawka Rymanowska, fragments of wood at Błażowa, Jamna Dolna 2 and Wola Czudecka, as well as leaves and fragments of twigs at Jamna Dolna 2. If such fragile objects as dragonflies, particularly susceptible to destruction, sank to the bottom, the same could have happened with fishes (dead or alive). Directional orientation of skeletons on bedding planes, which would indicate deposition of carcasses from bottom currents, does not occur in the fish-bearing layers studied, and has never been observed (see Jerzmańska and Kotlarczyk 1975; Kotlarczyk *et al.* 2006) in other parts of the Menilite-Krosno Series in Poland.

Some specimens of the families Clupeidae, Argentinidae, and Phosichthyidae from Jamna Dolna 1 and of the families Clupeidae and Bathylagidae from Jamna Dolna 2 have strongly deformed vertebral columns. This indicates either a large distance (probably vertical) from the place of their death to that of burial or a long period of time between death and burial.

Environment at the burial place and its surroundings

Analysis of the states of preservation of the disarticulated skeletons suggests that the carcasses decayed at the burial place under quiet conditions. Only in rare cases are there indications of current action or scavenging.

Carcasses of different fish taxa do not decay in the same way, as shown by Schäfer (1972) in experiments on Recent forms. This is due to:

- physical and chemical factors, such as temperature, pressure, alkalinity, salinity, presence/absence of oxygen;
- anatomy of fishes, because carcasses of different fish species decay variably and over different periods of time despite almost equal external conditions; moreover, distinct differences may appear between specimens of the same species, for example with respect to the quantity of undigested food in its intestines.

As a result of decay of soft tissues, the scales and bones detach and the skeleton disintegrates. Disarticulated bones and scales are easily transported, and abraded or dissolved. Usually, in the inital stage of disarticulation, the body cavity breaks open due to the development of gases, the scales detach and the skull disarticulates. Scales do not detach simultaneously, but gradually, usually in the abdominal region at first, and afterwards in the caudal region. The sequence of disarticulation of particular parts of a fish may be variable.

Each of the ichthyotaphocoenoses BJ.9, BJ.7, BJ.5, BJ.4, JD1.B, JD1.C, JD1.D, JD1.E, JD1.E1, JD2.K, JD2.LG, JD2.Z, JD2.X, RU.34, RU.32, RU.WAP1, RU.WAP2, WO and WU is derived from deposits that record a relatively long period of time (from a thousand to a few hundred thousand years), and therefore has features typical of a necrocoenose. If an ichthyotaphocoenose contains fishes of a single family in at least three different stages of skeleton disarticulation, it resulted from either changeable physico-chemical conditions, or a varied sedimentation rate, or varied frequency of deaths. A predominance of articulated skeletons (stage 5) in ichthyotaphocoenoses RU.WAP1 and RU.WAP2 indicates permanent stable conditions leading to well-preserved fishes. Such a state of preservation in these two ichthyotaphocoenoses, preserved in laminated limestones interpreted as of pelagic origin, may be due to the precipitation of calcium soap (adipocere) in the soft tissues of a fish at its burial place. Such precipitation was observed in Recent fish by Berner (1968). It is noteworthy that the state of fish preservation (a high percentage of disarticulated skeletons) in one of the localities studied (Rudawka Rymanowska) is much worse in the shales than it is in the limestones. Consequently, it is most likely that the sedimentation rate of the calcareous ooze was much higher than that of the pelitic, terrigenic particles.

The presence of articulated skeletons in deposits of low sedimentation rate indicates anoxic conditions in the sediment and bottom waters (see Schäfer 1972; Allison and Briggs 1991; Behrensmeyer 1991). The toxic conditions near the bottom did not allow for scavenger activity. However, it should be noted that soft tissues decay in both oxygenated and anoxic waters (Allison 1988; Allison and Briggs 1991), though the intensity of decay is much lower in the latter (Schäfer 1972).

The presence of layers and laminae of grey shales in the fish-bearing section at Błażowa indicates periodic changes in the chemocline, specifically an increase in oxygenation in, and above, the sediment/water interface at the burial place. The same is indicated at Jamna Dolna 2 by the presence of burrow-bearing layers in green shales. The abundance of fishes of the family Syngnathidae and algae at Jamna Dolna 2, and of the latter at Błażowa, allows recognition of algal communities in the near-surface waters. These fishes and algae may well have been derived from communities similar to those in the Recent Sargasso Sea, which have been recorded (Jerzmańska and Kotlarczyk 1975, 1976, 1988, 1991; Kotlarczyk 1991; Kotlarczyk *et al*. 2006) in the Oligocene deposits of the Menilite Formation.

The presence of the Centriscidae, which are reefal, neritic and epipelagic (0–300 m) and confined to warm tropical waters, at Jamna Dolna 1 and Wujskie, indicates warm near-surface waters (Jerzmańska and Kotlarczyk 1968) during sedimentation of the deposits of the Jamna Dolna Member, Kotów Chert Member (Early Rupelian), and Wujskie Limestone Horizon (Late Rupelian). The occurrence of Syngnathidae, which are epipelagic (0–300 m) and usually occur among algae or seaweeds, at Jamna Dolna 1 suggests floral communities in near-surface waters.

Preservation of fishes in some other Oligocene–Miocene ichthyotaphocoenoses

Numerous Oligocene–Miocene ichthyotaphocoenoses have long been subjected to very detailed taxonomic studies, albeit data on their preservation and/or taphonomy are either very scarce or lacking altogether.

Oligocene–Lower Miocene of the Outer Carpathians: The state of preservation of fishes in the Tylawa Limestones (ichthyotaphocoenoses RU.WAP1 and RU.WAP2) is markedly different from that reported formerly in the younger (see Text-fig. 3) Jasło Limestones (Jerzmańska 1960). In the latter, some skeletons have the vertebral column strongly deformed (see Jerzmańska 1960, p. 408, and pl. 5, fig. 2) and, moreover, preserved as either isolated skulls or headless trunks (see Jerzmańska 1960, p. 408, pl. 6).

Ichthyotaphocoenoses from the Ukraine (localities Borysław, Delatyn, Jasienica Solna, Majdan, Mikuliczyn, Tatarów, Pasieczna, river Lubiżnia, Spas; see Gorbach [Horbatsch] 1956, 1961) contain, like those studied herein, both articulated and variably disarticulated skeletons. The Clupeidae are usually more or less disarticulated and their vertebral columns are arched (see Gorbach [Horbatsch] 1956, 1961).

Ichthyotaphocoenoses from Romania (localities Bezdead, Gura Humorului, Homoraciú, Suslăneşti, Piatra Neamţ), like those studied herein, contain fishes having jaws agape (Paucă 1932, 1933; Jonet 1958; Ciobanu 1977) and disarticulated skeletons (Paucă 1933, Brustur and Grigorescu 1973). From Bezdead and Suslăneşti, Paucă (1932, 1933, 1934) reported many fishes having the vertebral column arched, such as the moderately elongate and narrow-bodied specimens, mainly of the families Clupeidae and Serranidae. Most of the disarticulated skeletons had disintegrated in a quiet environment, but the state of preservation of some skeletons is interpreted as a result of macroscavenger activity, presumably of crabs.

Ichthyotaphocoenoses from Piatra Neamţ, described by Ciobanu (1977), differ from most of those studied herein in the predominance of articulated skeletons, and fishes having a straight vertebral column. They are similar in the presence of fragments of skeletons.

Oligocene of the Rhine Graben: Ichthyotaphocoenoses from the Rhine Graben in France (locality Froidefontaine) and Germany (locality Frauenweiler, Wiesloch area) differ from those studied herein in the presence of more or less articulated skeletons of cartilaginous fishes (see Pharisat 1991; Micklich and Parin 1996; Hovestadt and Hovestadt-Euler 1999).

Oligocene of the Caucasus: Ichthyotaphocoenoses from the Caucasus (locality Sukmei-don, Russia) are similar to those studied herein in the abundance of variably disarticulated skeletons, deformations of vertebral columns, and the presence of fragments of skeletons (see Hecker and Merklin 1946). Moreover, disarticulated skeletons are associated with articulated ones. The ichthyotaphocoenoses contain fishes with a deformed or straight vertebral column. In the localities Bielaya River and Sukmei-don, the ichthyotaphocoenoses differ from those studied herein in the preservation of otoliths *in situ*, as reported by Rozenberg and Prokofiev (2004) for the order Gadiformes.

Miocene of the Caucasus: Ichthyotaphocoenoses from the Caucasus (locality Chernaya Rechka, Russia), like the Oligocene ones (from Sukmei-don), are generally similar to those studied herein. There is a high density of skeletons of the Centriscidae, as in ichthyotaphocoenose WU.1, but the fish-bearing deposit is coarser-grained and contains mica flakes, suggesting current (? turbidity) deposition (see Hecker and Merklin 1946). Some specimens of Centriscidae from the Caucasus have their first dorsal spine angled ventrally, a feature is absent in specimens studied herein.

CONCLUSIONS

The spatial arrangement of disarticulated skeletal elements of fishes in close proximity to the articulated portion of an individual indicates that disarticulation in all 19 studied ichthyotaphocoenoses resulted from the decay of soft tissues at the burial place, in a calm environment. Some cases may indicate the activity of macroscavengers or bottom currents.

All of the ichthyotaphocoenoses originated as a result of long-term accumulation of carcasses at the burial place, under low rates of sedimentation, representing condensation events.

The preservation of more or less articulated skeletons resulted from the prevalence of anoxic conditions in, and just above, the sediment/water interface.

Exceptionally good preservation of skeletons in the Tylawa Limestones has presumably resulted from the precipitation of calcium soap (adipocere) in the soft tissues of fish carcasses at the burial place.

All of the 19 ichthyotaphocoenoses display characters indicative of mass mortality of fishes (high density of individuals, and/or the presence of individuals with jaws agape, and/or high number of juveniles), but none of these characters is decisive unequivocally. It is most likely that only some individuals died suddenly during mass mortality events, whereas the majority died over a period of time as a result of senility, diseases, and other circumstances still unrecognized. Generally, all of the ichthyotaphocoenoses display characters of mixed assemblages, and they show features characteristic of both necro- and of thanatocoenoses. Probably most of the fishes lived in the water above the deposition site and the carcasses sank to the bottom after death. However, the presence of associated flora and fauna, i.e., amphipods, land-derived dragonflies and bird feathers, indicates that the taphocoenoses originated as a result of transport (vertical and/or horizontal) of biotic remains from various environments. Both the fishes and the associated remains settled onto the sea bottom successively (over time), and thus their assemblages acquired features typical of necrocoenoses. Throughout the whole Menilite-Krosno Series, taphonomical variability/succession cannot be demonstrated.

Unusulal cases of preservation of the fish, such as these choked to death on a smaller one, or those fish containing a prey fish in its intestines, reported formerly (Bieńkowska 2002, 2004b), are interpreted as an evidence of predation recorded for the first time in the Menilite-Krosno Series of Poland.

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