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CLUPEID SCALES FROM THE MENILITE BEDS (PALAEOGENE) OF THE CARPATHIANS

Abstract. — A reconstruction of the arrangement and variation of the scales in different parts of the body of the Carpathian Clupeidae, *Clupea sardinites* Heckel and *Alosa* cf. *sagorensis* Steindachner, has been made. The squamation of *Alosa* sp. is partially described. The taxonomy of the species is revised. *Alosa* cf. *sagorensis* Steindachner has not previously been recorded from the Menilite Beds, and it is suggested that clupeid scales may be useful for stratigraphical purposes in the Carpathians.

INTRODUCTION

The Menilite Beds of the Carpathian flysch have long been known to contain numerous fossil fish and scales (Heckel 1850; Rychlicki 1909; Paucă 1934; Kalabis 1948; Horbatsch 1956; Jerzmańska 1960 and others). More recent studies (Jerzmańska and Kotlarczyk 1968; Jerzmańska 1968) show three successive depthrelated assemblages of ichthyofauna. The lower bathypelagic assemblage is followed by the neritic-sublittoral assemblage which is, in turn, overlain by the upper bathypelagic assemblage. Recently, Kotlarczyk and Jerzmańska (1976) have suggested a more detailed ichthyo-stratigraphy, distinguishing six zones. The lowermost zone, IPM 1, corresponds with the distribution of the lower bathypelagic assemblage. The second zone, IPM 2, corresponds with the neritic-sublittoral assemblage and zones IPM 3 to IPM 6 correspond to the upper bathypelagic assemblage. The zones can be recognized by index taxa, but other taxa, which include representatives of the family Clupeidae are larger varying. Complete skeletons are not found in all zones, but clupeid scales occur in large numbers. In the palaeoichthyological papers published so far lepidological problems have not been given much attention. Prof. Anna Jerzmańska, who has collected a large number of clupeid scales showing considerable morphological variation, encouraged me to study the stratygraphic significance of clupeid scales with Menilite Beds.

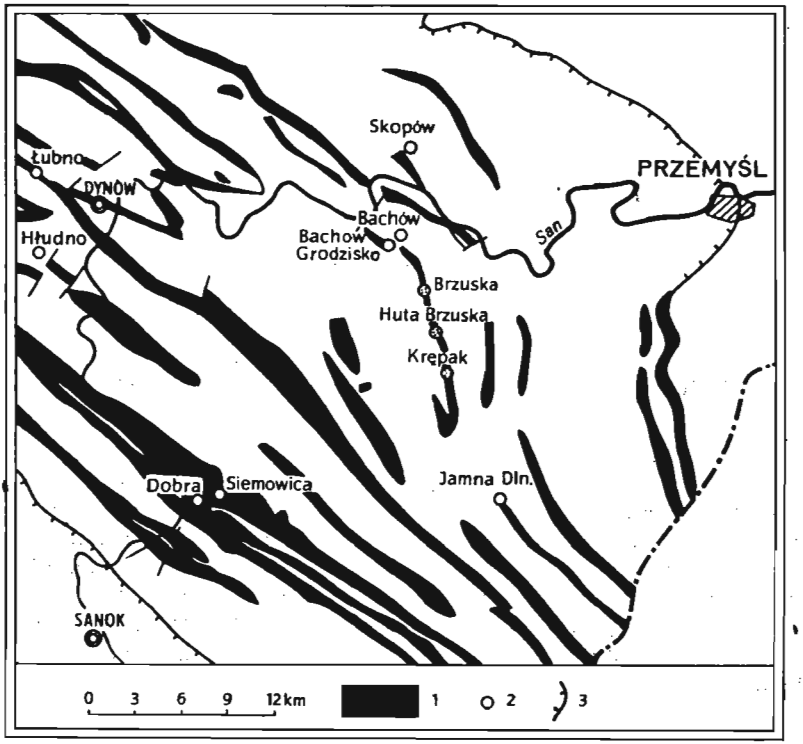

Fig. 1. Distribution of the localities with scales in the Skole unit (after Kotlarczyk and Jerzmańska 1976, simplified); 1 outcrops of the Menilite beds, 2 localities, 3 tectonic boundaries of the Skole unit.

Initially I studied material from the lower and upper bathypelagic assemblages. Comparative material from the neritic — sub-littoral assemblage was made available by W. Gawlikowski (1976) (Department of Palaeozoology, Zoological Institute of Wrocław University, Wrocław).

Synonyms given in the text have been established on the basis of scale structure.

Acknowledgements. — I wish to express my cordial thanks to Prof. Anna Jerzmańska (Department of Palaeozoology, Zoological Institute, University of Wrocław) under whose help and guidance the present study has been carried out, for making available to me the collections of Carpathian clupeids and their scales. Cordial thanks are also due to Prof. Janusz Kotlarczyk (Institute of Geology and Mineral Deposits, Academy of Mining and Metallurgy, Cracow) for showing me the sites and explaining the geology of the Carpathians. I wish to extend my thanks also to Prof. A. N. Svetovidov (Zoological Institute of the Academy of Sciences USSR, Leningrad) for allowing me to study the collections of Recent clupeid fish as comparative material. I thank Mr. Z. Staniewski, M. Sc. for making the photographs.

Table 1

Locations of outcrops in the Menilite Beds

Assemblages	Zones	Localities	Number of scales
upper bathypelagic	IPM 6	Bachów I	600
		Krępak	223
		Brzuska	12
		Hłudno	162
	IPM 5	Huta Brzuska	43
		Krępak	11
	IPM 4	Sobniów	11
		Łubno	13
		Hłudno	10
	IPM 3	Krępak	41
neritic sublittoral	IPM 2	Jamna Dolna (D—H)*	
lower bathypelagic	TPM 1	Skopów	1230
		Bachów Grodzisko	108
		Jamna Dolna (A—C)	192
			2656

* After Gawlikowski (1976)

MATERIAL

The present study is based on material collected from the Palaeogene Menilite Beds in the north-eastern part of the Carpathian flysch (table 1). The material was collected in the years 1971—1976 at the following sites (Skole Unit): Bachów I, Bachów Grodzisko, Krępak, Huta Brzuska, Brzuska and Hłudno. In addition, I used material gathered earlier by Prof. A. Jerzmańska from: Jamna Dolna (A—C), Skopów, Łubno (all from Skole Unit), Sobniów (Silesian Unit). The distribution of these sites in the Skole Unit is shown in figure 1. A detailed geological description of the sites and the ichthyofauna present can be found in: Sobniów — Jerzmańska (1960), Łubno — Jerzmańska and Jucha (1963), Jamna Dolna — Jerzmańska and Kotlarczyk (1968), Skopów, Krępak — Jerzmańska (1968), Bachów I — Jerzmańska and Kotlarczyk (1975), Brzuska, Huta Brzuska, Bachów Grodzisko, Hłudno — Jerzmańska and Kotlarczyk (in preparation). The fish and scale specimens are housed in the Department of Palaeozoology, Zoological Institute of Wrocław University (abbreviated as Z. PAL. WR.).

Table 2

Percentages of scales of different species of Clupeidae in successive zones of the Menilite Beds

Zones	*Clupea sardinites* %		*Alosa cf. sagorensis* %	*Alosa sp.* %
IPM 6	thin scales; no differentiation of scales in posterior part of body	ca 50	ca 10	ca 40
IPM 5		ca 50		ca 50
IPM 4		100		
IPM 3		ca 60	ca 10	ca 30
IPM 2		100*		
IPM 1	thick scales; differentiation of scales in posterior part of body	100		

* After Gawlikowski (1976)

Table 3

Differentiation of scales of *Clupea sardinites* Heckel in the vertical profile of the Menilite beds

	scales of Clupea sardinites	region I	region II	region III	the posterior part of body
ZONES	IPM 6	•	•	• •	• •
	IPM 5	•	•	• •	• •
	IPM 4	•	•	•	• •
	IPM 3	•	•	•	• •
	IPM 2	•	•	• •	• •
	IPM 1	•	•	• •	• • • •

Data from unpublished manuscript of Gawlikowski (1976)

STRUCTURE AND DIFFERENTIATION OF CARPATHIAN CLUPEID SCALES

Clupeid scales easily fall out of the scale pockets, so that isolated scales are common as fossils. Fishes with preserved squamation are rare, as are patches of intact squamation.

Scales from the Carpathian Menilite Beds show both layers that make up the scale of living clupeid fish: the hyalodentine and lamellar layers. Impressions of scales are uncommon. During cleaving of the rock the two scale layers easily separate, so that each is seen from the medial side. However, all the morphological features of modern scales can be seen (fig. 2).

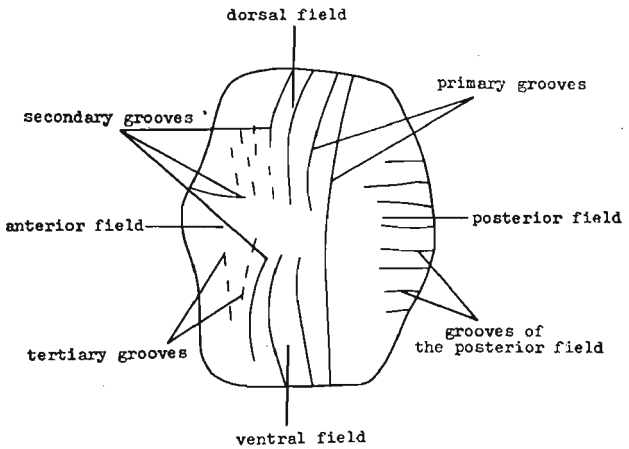

Fig. 2. Diagram of the scale of Clupeidae (dorsal and ventral fields are lateral fields of scale).

The hyalodentine layer of modern clupeids, being the thinner outer layer of the scale, shows striae, grooves and annuli. However, the shape of these elements on the unexposed portion of the scale differs from that on the exposed part. Striae are restricted to the anterior, unexposed part of the scale, as fine hyalodentine swellings, closely arranged, straight or slightly curved, and running vertically. Grooves are found in both the exposed and unexposed parts, and they correspond to gaps in the hyalodentine. The grooves on the exposed part have a fairly uniform shape, as long or short horizontal lines. The grooves of the unexposed part show considerable variation in shape and length. In addition to primary and secondary grooves distinguished by Lagler (1947), there may be short, straight radial or vertical tertiary grooves (Szymczyk, in press). In the clupeids, the annuli are only marked on the unexposed part of the scale, and in the majority of forms they are poorly developed.

These characteristics may also be seen in the hyalodentine of the

Carpathian clupeids (pl. 58: 1). The striae are always distinct, but the grooves are poorly marked and appear as fine cracks, while the indistinct annuli are only sporadically noticeable.

The inner, lamellar layer of the scale of living clupeids is made up of numerous lamellae. This layer is always much thicker than the hyalodentine. A similar relationship has also been found in the Carpathian clupeids. Variation is also observed in the thickness of the lamellar layer, depending on the age of he sediments investigated, as noted by Paucă (1934).

On the medial surface of the lamellar layer the course and arrangement of the hyalodentine grooves is very distinct. The grooves here are represented by swellings (pl. 58: 2, 5, 6) and at the same time by notches (pl. 58: 3) on the underside of the lamellar layer. Scales showing the lower surface of the lamellar layer are very rare in the Carpathians. On the medial side of the lamellar layer some scales (cf. p. 12) possess nodules as extensions of the grooves, or grouped together on the central portion of the scale (pl. 58: 4).

The variable thickness of the lamellar layer clearly affects the preservation of the scales in both bathypelagic assemblages. Scales of *Clupea sardinites* Heckel from the IPM 1 zone appear well preserved and are characterized by strong swellings of the lamellar layer. However, the thinnest scales of the same species from the upper bathypelagic assemblage are poorly preserved.

The mainly isolated Carpathian clupeid scales are diverse in shape, groove arrangement and form of the posterior edge. Most of the scales are clypeate in shape and elongated vertically (pl. 58: 3). Scales of a rounded shape (pl. 58: 6), triangular (pl. 58: 1, pl. 59: 1) or irregular (pl. 58: 5) are less numerous. The arrangement of grooves is most often simple, but their course is fairly variable: vertical (pl. 58: 3), horizontal (pl. 58: 2), radial (pl. 58: 1), oblique or mixed (pl. 58: 5, pl. 59: 2). Less frequently they form a reticulate pattern (pl. 59: 1). The posterior edge of the scales is smooth (pl. 58: 3, 6) or crenellated (pl. 59: 2, 3).

The ichthyological literature contains no comparative data that would make it possible to evaluate the taxonomic importance of such variations. Although some investigators (Peabody 1928; Zamakhayev 1951) assume that the scales of modern clupeids are of diagnostic importance, as they permit identification of genera and sometimes even species, these conclusions are not satisfactorily documented. It was, therefore, necessary to find out to what extent scale diversity reflects taxonomic differentiation. Comparative studies of modern Clupeidae enable me to show that differences in scale morphology are connected with their distribution on the lateral surfaces of these fish (Szymczyk, in press). Scales within each region are similar in shape, and are characteristic of the particular region. Hence,

isolated fossil scales may be identified as belonging to a particular part of the body. However, this was insufficient for a complete reconstruction of the squamation of the Carpathian clupeids. A more exact interpretation of the distribution and size of the body regions of these fish was only possible after a few specimens had been found with well preserved squa-

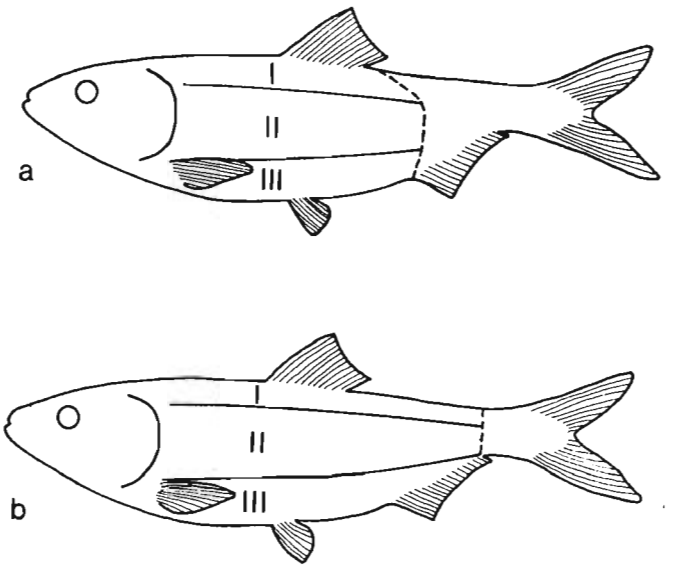

Fig. 3. Plan of division on the three regions of the lateral parts of the body of Carpathian Clupeidae: *a Clupea sardinites* Heckel, *b Alosa* cf. *sagorensis* Steindachner; I dorsal, II medial, III ventral. Broken lines show, probably, the limits of scales covering the posterior part of body.

mation. On the lateral surfaces of the fossil forms, three distinct regions could be distinguished: I — dorsal, II — medial, III — ventral (fig. 3). The posterior portion of the body could not be fully reconstructed.

Studies of modern Clupeidae show that scales in body region II show the least variability of morphological features (Szymczyk, in press), and may, therefore, be used in taxonomic considerations. These studies have also demonstrated that region II comprises the largest number of lateral series of scales. Thus the fossil scales of this region should be most numerous. These relationships are in fact found for the most abundantly represented scales of *Clupea sardinites*.

Occasionally even a single, isolated scale may provide information on the structure of the soft parts of the body of a fish. An example is the asymmetric scales with a long posterior process which occur only in the deep, horizontal groove found immediately behind the base of the pectoral fins in some modern clupeids (Szymczyk, in press). Isolated fossil scales of this type thus indicate that this groove existed in extinct forms (cf. p. 13 and 18).

SYSTEMATIC PART

Order **Clupeiformes**
Suborder **Clupeoidei**
Family **Clupeidae** Bonaparte, 1831

Remarks. — It has long been considered that in the Carpathians, the family Clupeidae is represented by the genus *Meletta* Cuvier and Valenciennes (Heckel 1850; Rychlicki 1909; Weiler 1928; Gofstheyn 1953). All clupeid scales were given this generic name, which has also been introduced into the geological literature, where the Menilite Shales were called the "Melettaschiefer". The name has persisted even after fossil forms of the genus *Meletta* had been recognized to be congeneric with *Clupea* Linné (Simionescu 1905; Paucă 1929). This genus, with the single species *Clupea sardinites*, is the only representative of the subfamily Clupeinae in the Menilite Beds. Greater taxonomic diversity of Clupeidae begins only in the neritic-sublittoral assemblage (zone IPM 2), from which skeletons of *Alosa sculptata* Weiler (Paucă 1934) and *Pomolobus* sp. (Jerzmańska 1968) of the subfamily Alosinae are known. Scales of this subfamily occur in large numbers in the upper bathypelagic assemblage (table 2).

Subfamily **Clupeinae**
Genus *Clupea* Linné, 1758
Clupea sardinites Heckel, 1850
(pl. 58: 1—3, 5, 6; figs 4, 5)

1850. *Meletta sardinites* Heckel: 230, pl. 24.
1850. *Meletta longimana* Heckel: 231, pl. 25: *b*—*i*.
1850. *Meletta crenata* Heckel: 233, pl. 26: *b*, *c*.
1928. *Meletta* sp.; Weiler: 69, figs 10, 11.
1934. *Clupea* sp.; Paucă: 35, fig. 6.
1953. *Meletta* sp.; Gofstheyn: 99, fig. 2.
1958. *Clupea* sp.; Jonet: 35, figs 11, 13.
1958. *Alosa* sp.; Jonet: 39, figs 15, 16.
1958. *Alosa crassa* Sauvage; Jonet: 40, fig. 17.

Material. — 2132 isolated scales (from the IPM 1 — IPM 6 zones), several pieces of squamation, and 5 complete skeletons with preserved squamation (Jamna Dolna — Z. Pal. Wr. A/349, 355, 362; Krępak — Z. Pal. Wr. A/2037; Huta Brzuska — Z. Pal. Wr. A/2039).

Description. — Scales with clearly marked grooves and a smooth posterior edge. The lamellar and hyalodentine layers vary with the age of the sediments (cf. p. 5). In the deepest part of the body, anterior to the dorsal fin, the number of scales in a vertical series reaches 12. The diversity of the shape and distribution of the grooves on the scales of *Clupea sardinites* is connected with the regions of the surface of the fish. Figures 4 and 5 represent a reconstruction of the squamation.

In region I clypeate scales are found with vertical primary and secondary grooves broken in the middle. The two lateral fields of a scale have a different number of grooves (fig. 4*a*—*b*). Within this region some of the scales have longer grooves on the dorsal side than on the ventral side (fig. 4*a*).

Region II is also characterized by clypeate scales, but the vertical primary and secondary grooves, broken in the middle, are usually distributed symmetrically. The number of grooves varies between 2 and 6; in the anterior portion of this region, from

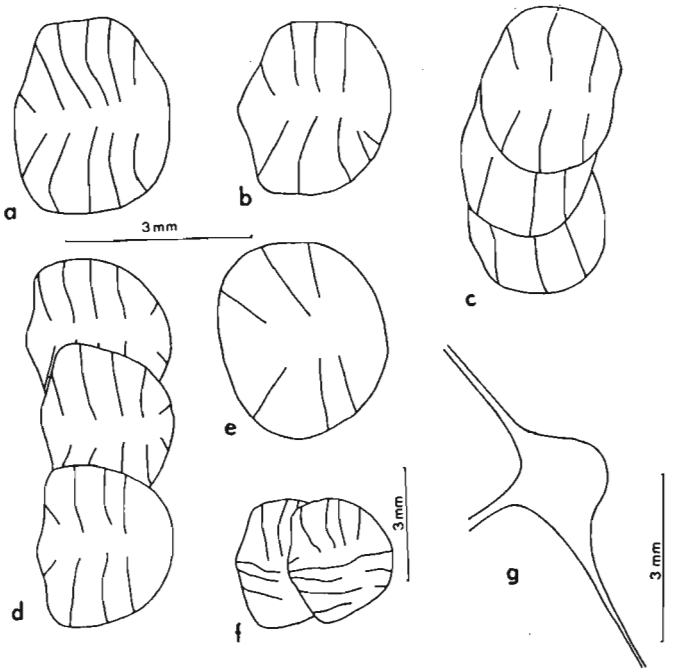

Fig. 4. Scales in *Clupea sardinites* Heckel: from region I (*a* Z. Pal. Wr. Ł/80, *b* Z. Pal. Wr. Ł/192); from region II (*c* Z. Pal. Wr. Ł/188, *d* Z. Pal. Wr. Ł/78); from region III (*e* Z. Pal. Wr. Ł/168, *f* Z. Pal. Wr. Ł/220); scute (*g* Z. Pal. Wr. Ł/168).

the head to the beginning of the dorsal fin, their number is small, 2 to 3 on one side of the scale (fig 4*c*). Only in the posterior part of this region are scales with larger numbers of grooves (up to 6) found (fig. 4*d*).

Region III is characterized by scales differing in shape and groove arrangement.

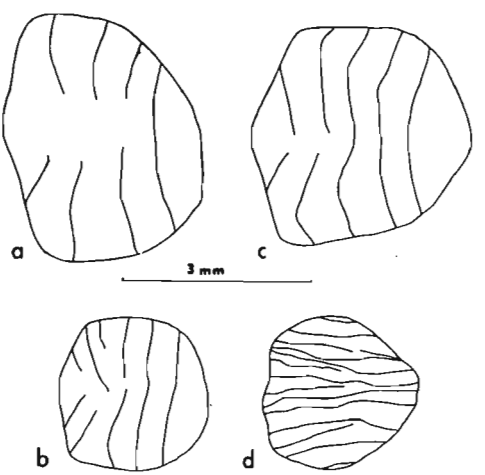

Fig. 5. Scales in *Clupea sardinites* Heckel from posterior part of body (*a* Z. Pal. Wr. Ł/61, *b* Z. Pal. Wr. Ł/192, *c* Z. Pal. Wr. A/2016, *d* Z. Pal. Wr. Ł/124).

Scales at the ventral body edge were clypeate with vertical and horizontal grooves (fig. 4*f*). Vertical grooves, which are short, are on the dorsal lateral field. The remaining part of the scale is occupied by primary and secondary horizontal grooves, extending from the anterior edge of the scale. Other scales of this region are rounded or more triangular in shape, with the primary and secondary grooves, which have gaps in the middle, radially arranged (fig. 4*e*).

In the posterior part of the body of individuals from zone IPM 1, in continuation of region II, scales probably occurred with several grooves broken in the middle, and 1, 2 or 3 terminal continuous grooves (fig. 5*a*—*c*). In higher zones, only scales with a single terminal continuous groove are found (table 3). The dorsal and ventral edges of the body were covered with small scales possessing abundant, densely arranged horizontal grooves (fig. 5*d*).

Scutes. Fossil scutes are seldom encountered. According to Jerzmańska (1968), in *Clupea sardinites* scutes are only found between the head and the pelvic fins, their number there being about 13. Scutes of this form are thin, delicate, their base having the appearance of a uniform lamella (fig. 4*g*). Scutes were, therefore, unkeeled.

Remarks. — The above reconstruction of scale distribution has been based primarily upon the regularites observed in the Recent *Sardinella aurita* Valenciennes and *Opisthonema libertalis* (Günther). These species were selected because of the emphasis placed by Jerzmańska (1968: 392) on the similarity of *Clupea sardinites* Heckel to representatives of the genera *Sardinella* Valenciennes and *Opisthonema* Gill. These regularities concerned the following: in region I — asymmetry in the arrangement of the primary and secondary grooves; in region II — symmetry of the primary and secondary grooves, an increase in their number, and appearance of continuous grooves towards the tail; in region III — primarily the shape and groove arrangement (radial or mixed). The few complete skeletons found with preserved squamation, and the pieces of squamation examined, to some extent confirm the proposed reconstruction of scale distribution on the body of *Clupea sardinites*, especially with regard to regions II and III.

The most striking example of the variability of scales of this species in the Menilite Beds is the variation in thickness of the lamellar and hyalodentine layers. The thickest scales were found in IPM 1 zone. It seems that a thinner lamellar layer is found in the IPM 2 zone (Gawlikowski 1976), while in higher zones (the upper bathypelagic assemblage) the scales of *Clupea sardinites* are clearly thinner. It seems that the presence of a variable number of continuous grooves may indicate a greater morphological diversity of the scale of the caudal part of the body in older representatives of *Clupea sardinites* (zone IPM 1).

Clupea sardinites appears to be one of the very common forms in the Carpathians, being represented throughout the Menilite Beds (Jerzmańska 1968) as the only representative of the subfamily Clupeinae. So far, the presence of *Clupea voinovi* Paucă, described by Paucă (1929, 1934), has not been confirmed. Apart from the skeletons, many authors (Heckel 1850; Paucă 1934; Gofstheyn 1953; Jonet 1958) have also reported the presence in the Carpathians of scales which I regard, on the basis of the reconstruction presented above, as belonging to *Clupea sardinites*. Four of the drawings of *Meletta longimana* given by Heckel (1850: pl. 25: *c*, *e*, *f*) no doubt represent region III of *Clupea sardinites*, whereas the next three (*b*, *h*, *i*) are from the middle part of the caudal region of this species, and the last one (*d*) resemble the scales near the edges of the caudal region. In turn, all four scales of *Meletta sardinites* shown in Heckel's plate 24 derive from region III of *Clupea sardinites*, while his *Meletta crenata* scales (pl. 26: *b*, *c*) represent region II of *Clupea sardinites*.

Two scales of *Meletta* sp. illustrated from Menilite Beds in Roumania (Weiler 1928: 69, figs 10, 11) are also scales of *Clupea sardinites*, probably from region II (fig. 10), and from the posterior portion of region III (fig. 11).

Two of the three drawings of scales from Suslănești, reported by Paucă (1934: 35, fig. 6) as *Clupea* sp., represent *Clupea sardinites* (the scale on the left of the drawing belongs to region III, that on the right to the posterior part of the body).

The scale group which Jonet (1958) described as *Clupea* sp. in fact represents *Clupea sardinites* (Jonet 1958: 35, figs 11, 13). Other scales with very numerous grooves, identified by Jonet as *Alosa crassa* (*op. cit.*: 40, fig. 17), as well as some of *Alosa* sp. scales (*op. cit.*: 39, figs 15, 16), should be considered as derived from the posterior part of *Clupea sardinites*.

Almost all the scales described by Gofstheyn (1953: 107, fig. 2) as *Meletta* sp. no doubt represent scales of *Clupea sardinites* from regions II and III (except the seventh consecutive scale in this drawing, whose taxonomic position seems to be uncertain).

Subfamily **Alosinae**
Genus *Alosa* Linck, 1790
Alosa cf. *sagorensis* Steindachner, 1863
(pl. 58: 4; pl. 59: 3—5; figs 6, 7, 8a)

1938. *Alosa* cf. *sagorensis* Steindachner; Weiler: 10.

Material. — 80 isolated scales from the IPM 3 and IPM 6 zones: Bachów I, Krępak, Brzuska and Hłudno; 2 portions of squamation and 2 specimens with preserved squamation (Bachów I — Z. Pal. Wr. Ł/81; Krępak — Z. Pal. Wr. A/2015).

Description. — On the unexposed part of the scales, in addition to the primary and secondary grooves, nodules are present in the middle and lateral fields. The posterior edge of the scales is crenellated (pl. 59: 3). The number of scales in a vertical series below the dorsal fin is 10. The great diversity of these scales, in shape and arrangement of grooves and nodules, indicates that they come from different parts of the body. The squamation of this form is reconstructed in figure 7. On the basis of isolated asymmetric scales with a characteristic posterior process, I have assumed the existence of a groove in which the first ray of the pectoral fin was located (cf. p. 7).

There are clypeate and oval scales in region I. Oval scales, found only at the dorsal edge of the body, have oblique grooves in the lateral fields. There the nodules occupy the central part (fig. 7*a*). Clypeate scales cover the remainder of this region. Primary and secondary grooves are vertical in the two lateral fields, the last primary groove being continuous; in the dorsal lateral field it bends and joins the

Fig. 6. *Alosa* cf. *sagorensis* Steindachner: *a* scales from anterior part of region II (Z. Pal. Wr. Ł/24), *b* scutes (Z. Pal. Wr. Ł/4).

posterior edge. The nodules are most often found in continuation of the vertical grooves (fig. 7b).

Region II contains only clypeate scales with vertical primary and secondary grooves in the lateral fields. In the anterior portion of this region, all grooves have

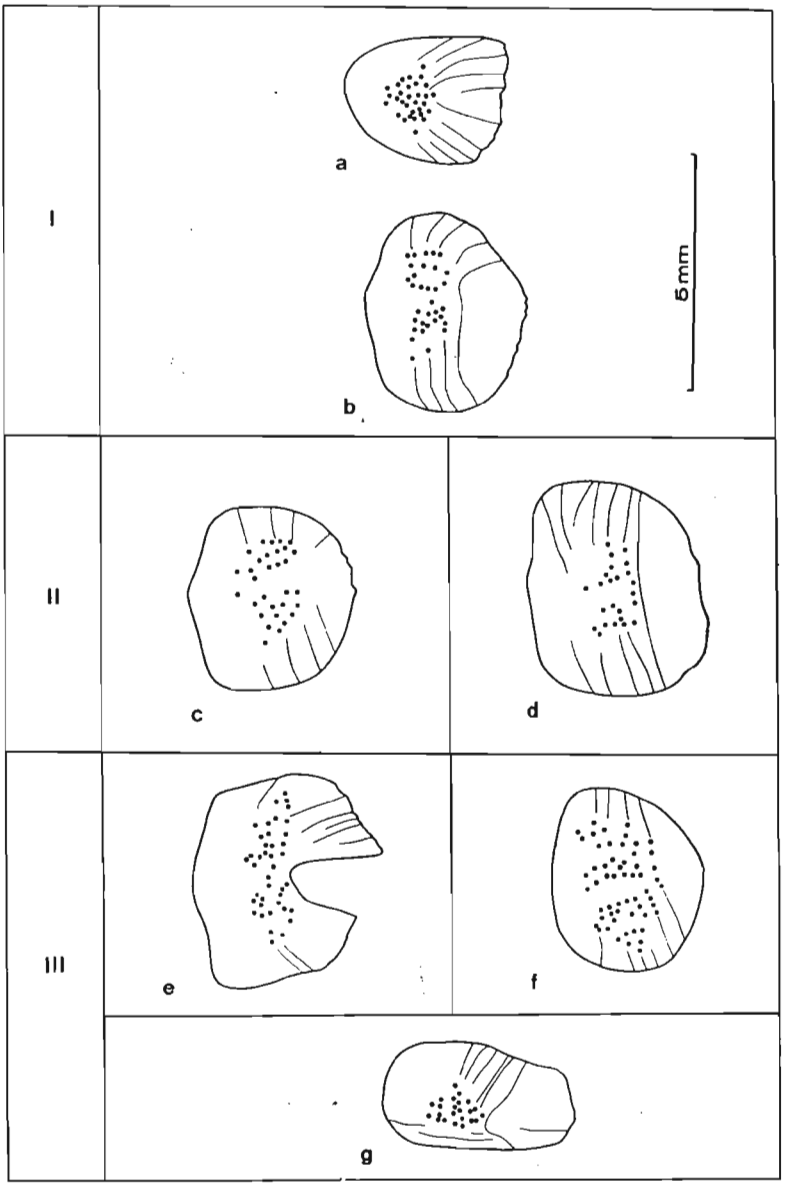

Fig. 7. Distribution plan of scales of different structures in individual region (I—III) and parts of regions (*a*—*g*) in *Alosa* cf. *sagorensis* Steindachner. I. *a* the scale from the dorsal margin of the body (Z. Pal. Wr. A/2015), *b* the scale near from the region II (Z. Pal. Wr. B/353), II. *c* the scale from the anterior part of the region (Z. Pal. Wr. Ł/4), *d* the scale from the middle part of the same region (Z. Pal. Wr. Ł/4), III. *e* the scale covering the groove (Z. Pal. Wr. Ł/3), *f* the scale from the middle part of the region (Z. Pal. Wr. Ł/4), *g* the scale from the ventral margin of the body (Z. Pal. Wr. Ł/6).

gaps. Nodule groups in both lateral fields are separated by a smooth surface in the middle of the scale (figs 6*a*, 7*c*). In the posterior part of this region the grooves are more numerous and longer, the last primary groove being continuous. There are a few nodules in the middle (fig. 7*d*).

Region III. The scales of this region show the highest diversity in the shape and the arrangement of grooves and nodules.

1) The pectoral fin area. — Immediately behind the base of the pectoral fins a horizontal groove probably occurred covered with asymmetric scales (fig. 7*e*). The grooves in both the lateral fields of these scales are few and oblique. The grooves of the posterior field are horizontal. The nodules are grouped in the central portion.

2) Scales at the edge of the belly. — These are elongated horizontally, with a straight ventral margin and a rounded dorsal margin. The primary and secondary grooves in the dorsal lateral field are vertical, the last groove being continuous and semicircular. In the ventral lateral field, the grooves run horizontally. The central portion of the scale is filled with vertical series of nodules (fig. 7*g*).

3) The remainder of this region was covered by rounded scales. Short, vertical grooves are few in this area, and are found in the lateral fields. Nodules occur in very large numbers, forming vertical series, filling the space between groove pairs (fig. 7*f*).

Scutes. Scutes are found partially preserved on fossil specimens. They are thick and solid, with strongly convex bases, forming a clear keel (fig. 6*b*).

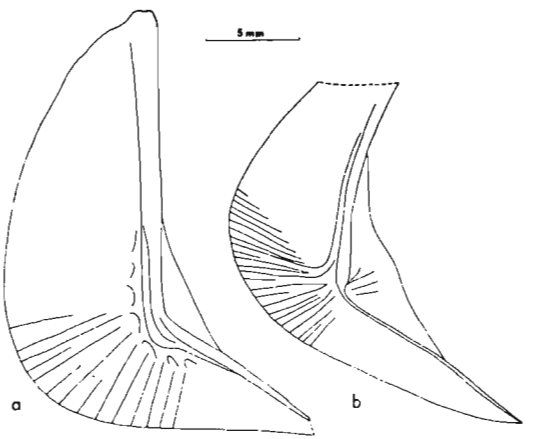

Fig. 8. Praeoperculum: *a Alosa* cf. *sagorensis* Steindachner (Z. Pal. Wr. Ł/3), *b* Alosa sp. (Z. Pal. Wr. Ł/7).

Remarks. — The squamation of *Alosa* cf. *sagorensis* was unusually close, because it is preserved intact in fossil specimens. Detached scales are nearly always found around skeleton parts so that it was possible to make a relatively accurate reconstruction of particular regions. Variations observed in a living alosin, *Brevoortia tyrannus* (Latrobe) were also found (Szymczyk, in press). These variations concern the distribution of tertiary grooves on the scales from different regions of this fish, namely: in region II — the presence of numerous tertiary grooves and their distribution in the lateral fields in the anterior scales of this region (posterior scales have a much smaller number of tertiary grooves); in region III — the presence of very numerous tertiary grooves, and their arrangement in series, most often in continuation of the corresponding vertical groove pairs. Although nodules are seen only in the

lamellar layer of the scales (cf. p. 5) their arrangement shows a certain similarity to the arrangement of the tertiary grooves. This made it possible to allocate isolated scales with nodules to the appropriate regions (partly II and III).

The number of asymmetric scales in the groove underneath the first ray of the pectoral fins in some living alosines is small, varying between 3 and 6, depending on the length of the groove (Szymczyk, in press). For this reason, these scales are rarely found in the fossil state. One such scale has been found in the material from Bachów I (Z. Pal. Wr. Ł/3; fig. 7e), side by side with bones of *Alosa* cf. *sagorensis* and other scales with nodules (pl. 59: 5). In contrast to the scales of this type found in modern clupeids, this scale is more rounded, its dorsal part is broader, and it is only slightly elongated.

As can be concluded from the above description, the most characteristic feature of the scales of *Alosa* cf. *sagorensis* is the presence of numerous and distinct nodules. However, forms with scales of this structure are not known among living clupeids. Only in the palaeontological literature can a few notes be found concerning the presence of nodules on the scales in some genera of the family Clupeidae. The youngest scales with nodules were found in Pliocene sediments in Roumania by Weiler (1928), who identified them as *Alosa* sp. According to Arambourg (1925, 1927), nodules are found in two Miocene forms, *Etrumeus boulei* Arambourg and *Alosa elongata* Agassiz. Arambourg did not analyse in detail the squamation of these two species, and only included drawings of two scales clearly differing in shape and nodule distribution (Arambourg 1925: 49, fig. 2). In *Etrumeus boulei* all nodules are grouped in the central portion of the scale, while in *Alosa elongata* they are situated in continuation of the numerous vertical grooves. Paucă (1934) was the first to report the presence of scales with nodules in the Oligocene clupeids. He identified them as *Alosa* sp. (*Etrumeus* ? sp.). The incomplete description of these giant scales (2 cm diameter) and the diagrammatic drawing (Paucă 1934: 39, fig. 9) do not resemble the scales of the two Miocene species mentioned above, or the scales from the upper bathypelagic assemblage. In the very numerous, small nodules and in size, they show some similarity to the scales of *Ganolytes aratus* (Jordan), a species related to the genus *Alosa* and known from the Miocene of California (David 1943).

In fin arrangement and distribution of grooves on the scales, *Alosa* cf. *sagorensis* from the Hungarian Oligocene (Weiler 1938) appears to be identical with the Carpathian forms described above. The pelvic fin base lies beneath the posterior part of the dorsal fin, whereas the beginning of the latter is above the 8th thoracic vertebra, as counted from behind. Weiler (1938) also stressed that the vertical grooves on the scales of the anterior part of the thorax are shorter and less numerous than those in the posterior part. Similar relations have been found in *Alosa* cf. *sagorensis* from the Carpathians. Moreover, Weiler (1938) thinks that a characteristic feature of *Alosa* cf. *sagorensis* scales is the presence of small, dispersed structures, which in the Hungarian specimens have the form of notches. In the Carpathian specimens these structures, which are associated with the lamellar layer, have resulted from the different state of preservation. In the Hungarian *Alosa* cf. *sagorensis* scales the structures in question, when viewed from the underside of the lamellar layer, appear to be notches, while in the Carpathian forms, in which the medial surface of the lamellar layer is seen, they have the appearance of nodules. We thus encounter a preservation similar to that in the notches and swellings on both surface of the lamellar layer in *Clupea sardinites* scales (cf. p. 5).

The similarity of the two forms is further indicated by the preoperculum (fig. 8*a*), which is strongly broadened at the angle, and the operculum with striae extending from the fovea glenoidalis (pl. 59: 4). Another characteristic feature of *Alosa* cf. *sagorensis* is the short and broad ramus horizontalis praeoperculi, whose length is equal to the maximum breadth of this bone.

Alosa sp.
(pl. 59: 2; figs 8*b*, 9, 10)

1934. *Clupea* sp.; Paucă: 35, fig. 6.
1958. *Clupea* sp.; Jonet: 35, fig. 12.

Material. — 444 isolated scales (from the IPM 3, IPM 5 and IPM 6 zones; Krępak, Huta Brzuska, Brzuska, Bachów I, Hłudno), 2 pieces of squamation and 3 incomplete skeletons with preserved squamation (Krępak — Z. Pal. Wr. A/2038; Huta Brzuska — Z. Pal. Wr. A/2040, Z. Pal. Wr. Ł/5).

Description. — The scales are thin, delicate and with crenellated posterior margins (pl. 59: 2). In the squamation of this form two types of scale with vertical grooves can be distinguished (fig. 9 *a*, *b*), differing in the presence or absence of horizontal grooves in the anterior field. In the first scale type the number of vertical grooves, broken in the middle, is 2 to 9. The number of horizontal grooves in the anterior field varies between 1 and 9 (usually 3 to 5). In the posterior field of the scales a few short horizontal grooves may be found (fig. 9*a*). The other scale type is also characterized

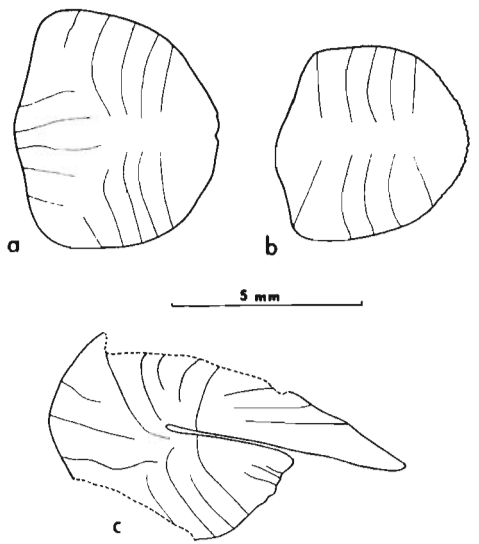

Fig. 9. Scales in *Alosa* sp. (*a* Z. Pal. Wr. B/117, *b* Z. Pal. Wr. Ł/9, *c* Z. Pal. Wr. Ł/12).

by broken vertical grooves, 3 to 6 in number. In this case, the posterior field is always devoid of grooves (fig. 9*b*).

Scale distribution. Scales of the two types occur alternately along the body, scales with horizontal grooves being much more numerous. This was seen in specimens with intact squamation and on pieces of squamation, and was confirmed by the fact that scales of both types are found scattered around the bones of a single individual. The fragment of squamation represented in figure 10*a*, probably comes from the anterior, mid-lateral region, as indicated by the relatively small number of horizontal and vertical grooves and the regular, almost symmetrical arrangement of the latter. The second piece, in which three morphological types of scale are found (fig. 10*b*), probably belongs to the ventral part of the body. It must be noted that it is in this area of the body of clupeids that the greatest diversity of scales, in shape and the course of the

grooves, is seen. In this specimen, scales are found with vertical and horizontal grooves, as well as scales without horizontal grooves in the anterior field. In the area of the pectoral fins, as in *Alosa* cf. *sagorensis* and other Alosinae, there was probably a horizontal groove for the first ray of the pectoral fins, covered by asymmetric scales with a long posterior process (fig. 9c). The grooves of both lateral fields run more or less vertically, whereas the grooves in the anterior field are horizontal.

Remarks. — So far the presence in the squamation of two types of scale, differing slightly in groove arrangement, has been found in two modern species of Alosinae (Szymczyk, in press): *Alosa sapidissima* (Wilson) and *Alosa pseudoharengus* (Wilson). In these species the majority of scales (so-called basic type) are found in regions II and III, separated in places by scales of different groove arrangement. The latter scales, less numerous, are commonest in the central part of the body, and rarer in the anterior and posterior parts of these regions. Similar relations in the fossil form are indicated by the above-described pieces of squamation including scales of 3—4 lateral

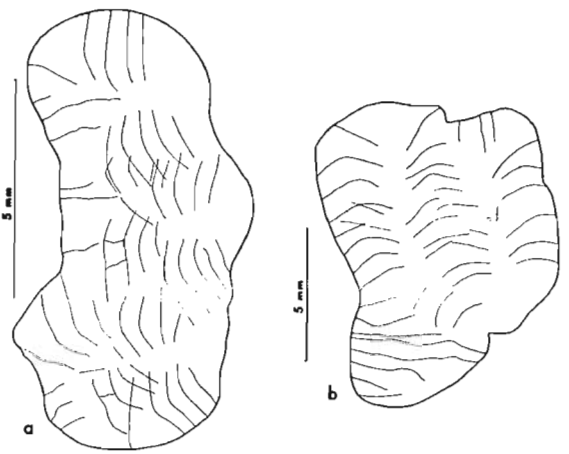

Fig. 10. Fragments of squamation of *Alosa* sp.: *a* from the mid-lateral area of the body (region II) Z. Pal. Wr. Ł/57), *b* from ventral part of the body (region III) (Z. Pal. Wr. B/171).

series. It seems, therefore, that the form described may be considered a representative of the genus *Alosa*. Apart from this, in the two living alosines there is a deep groove, covered by characteristic, asymmetric scales with a long posterior process, immediately behind the base of the pectoral fin (Szymczyk, in press). The occurrence of a scale of this shape in *Alosa* sp. indicates that the groove also existed in the fossil form (cf. p. 7). In contrast to the scale of *Alosa* cf. *sagorensis*, this scale has a typical shape, as in the modern Alosinae (cf, fig. 7*e* and fig. 9c). However, on the basis of a single scale it is difficult to ascertain if the groove was covered only by scales of the basic type (as in *Alosa pseudoharengus*), or by both scale types (as in *Alosa sapidissima*).

Apart from the structure of the squamation, the suggestion that this form belongs to the genus *Alosa* is further indicated by the presence (in the same layer — IPM 5 zone) of striated opercular bones. The shape of the proeperculum (fig. 8b), in particular, shows that these bones belonged to a species different from *Alosa* cf. *sagorensis*. The length of the ramus horizontalis is greater than the maximum breadth above the angle. Delicate radial striae are also found on the lower part of the ramus

verticalis. Because of the poor condition of the operculum, it is impossible exactly to describe the course of the striae on this bone. As there are no complete skeletons in the material studied, it is impossible to identify the form in question, so it has, for the time being, been described as *Alosa* sp. As has been mentioned above, this species occurred in material from the IPM 3, IPM 5 and IPM 6 zones.

Paucă (1934) included in his paper a drawing of a scale which he identified as *Clupea* sp. (*op. cit.*: 35, fig. 6; the central scale). However, I think that on account of the presence of vertical and horizontal grooves in the anterior field, it belongs to the above-described *Alosa* sp. A typical scale of *Alosa* sp. from the Menilite Beds in Roumania has also been illustrated by Jonet (1958: 35, fig. 12) who continued to call it *Clupea* sp. The detailed stratigraphic position of these Roumanian scales is not clear.

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REFERENCES

ARAMBOURG, C. 1925. Révision de Poissons fossiles de Licata (Sicile). — *Ann. Paléont.*, **14**, 2/3, 39—96.

— 1927. Les Poissons fossiles d'Oran. — Mater. Carte Geol. Algérie, sér. 1, Paléontologie, **6**, 1—298.

DAVID, L. R. 1943. Miocene fishes of southern California. — *Geol. Soc. Amer., Spec. Papers*, **43**, 1—181.

GAWLIKOWSKI, W. 1976. Zmienność kopalnych łusek Clupeidae z Karpat. — MS, Archiwa Instytutu Zoologicznego Uniwersytetu Wrocławskiego. Praca dyplomowa.

GOFSHTEYN, I. D. (ГОФШТЕЙН, И. Д.) 1953. О чешуе *Meletta* из черных сланцев Закарпатья. — *Тр. Львовск. геол. об., сер. палеонт.*, **2**, 99—110.

HECKEL, J. J. 1850. Beiträge zur Kenntniss der fossilen Fische Österreichs. — *Denkschr. kais. Akad. Wiss., Mat.-Naturw. Cl.*, **1**, 201—242.

HORBATSCH, L. P. (ГОРБАЧ, Л. П.) 1956. Ихтиофауна и условия образования отложений менилитовой серии Карпат. — Львовский Государственный Университет им. Ив. Франко. 1—12, Львов.

JERZMAŃSKA, A. 1960. Ichtiofauna łupków jasielskich z Sobniowa. — *Acta Palaeont. Pol.*, **5**, 4, 367—419.

— 1968. Ichtyofaune des couches à ménilite (flysches des Karpathes). — *Ibidem*, **13**, 3, 379—488.

— and JUCHA, S. 1963. Stanowisko ryb w łupkach jasielskich z Łubna koło Dynowa. — *Roczn. Pol. Tow. Geol.*, **33**, 2, 159—180.

— and KOTLARCZYK, J. 1968. Zespoły ichtiofauny z warstw menilitowych Karpat jako wskaźnik zmian środowiska sedymentacyjnego. — *Ibidem*, **38**, 1, 39—66.

— and — 1975. Kopalny zespół quasi-sargassowy z warstw menilitowych jednostki skolskiej Karpat polskich. — *Kwart. Geol.*, **19**, 4, 875—886.

— and — Stratygrafia warstw menilitowych synkliny Brzuski (Karpaty) na podstawie ichtiofauny (in preparation).

JONET, S. 1958. Contributions à l'étude des schistes disodyliques oligocènes de Roumanie. La faune ichthyologique de Homoraciu District de Prahova. 7—100, Lisboa.

KALABIS, VL. 1948. Ryby ze svetelnymi orgány z moravskeho paleogénu menilitovych břidlic. — *Čas. Zemsk. Musea v Brne*, **32**, 1—44.

KOTLARCZYK, J. and JERZMAŃSKA, A. 1976. Biostratigraphy of Menilite Beds of Skole Unit from the Polish Flysch Carpathians. — *Bull. Acad. Pol. Sci. Sér. Sci. Terre.* **24**, 1, 55—62.

LAGLER, K. F. 1947. Lepidological studies 1. Scale characters of the families of Great Lakes Fishes. — *Trans. Am. Microsc. Soc.*, **46**, 2, 149—168.

PAUCĂ, M. 1929. Vorläufige Mitteilung über eine fossile Fischfauna aus den Oligozänschiefern von Suslănęsti (Muscel). — *Bull. Sci. Acad. Roum.*, **12**, 4/5, 112—120.

— 1934. Die fossile Fauna und Flora aus dem Oligozän von Suslănęsti — Muscel in Rumänien. Eine systematische und paläobiologische Studie. — *Ann. Inst. Géol. Roum.*, **16**, 672—768.

PEABODY, E. B. 1928. The scales of some fishes of the suborder Clupeoidei. — *Univ. Color. Stud.*, **16**, 127—148.

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

SIMIONESCU, I. 1905. Sur quelques Poissons fossiles du Tertiare roumain. — *Ann. Sci. Univ. Jassy*, **5**, 1—17.

SZYMCZYK, W. 1978. Zróżnicowanie łusek u niektórych gatunków Clupeidae. — *Acta Univ. Wratisl.*, 437, Prace Zoologiczne, **9** (in press).

WEILER, W. 1928. Fische aus dem rumänischen Tertiär. — *Senckenbergiana*, **10**, 62—80.

— 1938. Neue untersuchungen an Mitteloligozänen Fischen Ungarns. — *Geol. Hungar., Ser. Palaeont.*, **15**, 1—31.

ZAMAKHAYEV, D. F. (ЗАМАХАЕВ, Д. Ф.) 1951. Розличе биологических показателей на чешуе с отдельных участков тела сельди. — *Тр. Московс. инст. рыбн. пром. хоз.*, **4**, 18—31.

WIESŁAWA SZYMCZYK

ŁUSKI CLUPEIDAE Z ZESPOŁÓW BATYPELAGICZNYCH WARSTW MENILITOWYCH KARPAT

Streszczenie

Badany materiał lepidologiczny pochodzi z paleogeńskich warstw menilitowych północno-wschodniej części Karpat fliszowych, z obszaru jednostki skolskiej (fig. 1). Obecność odrębnych zespołów ekologicznych: batypelagicznego dolnego, nerytyczno-sublitoralnego i batypelagicznego górnego wykazana przez Jerzmańską i Kotlarczyka (1968) oraz Jerzmańską (1968) wyłoniła potrzebę opracowania łusek Clupeidae w obrębie tych zespołów. W niniejszej pracy przedstawiono wyniki dotyczące tylko obydwu zespołów batypelagicznych.

Łuski Clupeidae masowo występujące w łupkach menilitowych zachowują obie warstwy budujące łuskę ryb współczesnych — hialodentynę i izopedynę. Stan za-

chowania łusek pozwala prześledzić wszystkie cechy morfologiczne obserwowane na łuskach współczesnych ryb śledziowatych. Łuski karpackich Clupeidae odznaczają się silnym zróżnicowaniem pod względem kształtu, układu rowków i wykształcenia brzegu tylnego (pls 58, 59), a niektóre z nich posiadają ponadto guzki widoczne tylko na powierzchni izopedyny. W oparciu o okazy z zachowanym pokryciem ciała i analizę morfologiczną pojedynczych łusek przeprowadzono rekonstrukcję okrywy łuskowej *Clupea sardinites* Heckel i *Alosa* cf. *sagorensis* Steindachner. Natomiast u trzeciej formy, *Alosa* sp., można było tylko częściowo zrekonstruować pokrycie ciała. Przy rekonstrukcjach tych wykorzystano ponadto pewne prawidłowości w rozkładzie i wykształceniu łusek zaobserwowane u współczesnych Clupeidae oraz ustalono synonimy łusek opisanych dotychczas z Karpat.

U *Clupea sardinites* brzeg tylny łusek jest gładki, a rowki wyraźnie zaznaczają się na powierzchni. Tylko u tego gatunku obserwuje się zmiany grubości łusek w zależności od wieku osadów. U osobników z dolnego zespołu batypelagicznego łuski są grube, natomiast w zespole batypelagicznym górnym łuski są wyraźnie cieńsze.

Łuski *Alosa* cf. *sagorensis* tworzące wyjątkowo zwartą okrywę ciała mają powycinany brzeg tylny, a na powierzchni izopedyny, obok rowków występują różnie rozmieszczone guzki (fig. 7). Obecność charakterystycznej, asymetrycznej łuski z okolicy płetw piersiowych (fig. 7: *e*) wskazuje na istnienie u tej formy bruzdy mieszczącej pierwszy promień płetw piersiowych. Gatunek ten, niepodawany dotąd z warstw menilitowych, stwierdzony został na podstawie analizy struktury łusek oraz kości pokryw skrzelowych.

Pokrycie ciała *Alosa* sp. tworzą dwa typy łusek różniące się obecnością lub brakiem rowków na polu przednim (fig. 9*a*, *b*). Łuski te są cienkie, o powycinanym brzegu tylnym. Podobnie jak u *Alosa* cf. *sagorensis* w okrywie łuskowej występowały asymetryczne łuski (fig. 9*c*) świadczące o obecności bruzdy w okolicy płetw piersiowych.

Zróżnicowanie gatunkowe przedstawicieli Clupeidae w profilu warstw menilitowych stwarza możliwość wykorzystania tych form i ich łusek do celów stratygraficznych (tab. 2).

Niniejsza praca została wykonana w ramach problemu międzyresortowego II/3.

ВЕСЛАВА ШИМЧИК

ЧЕШУИ CLUPEIDAE ИЗ БАТИПЕЛАГИЧЕСКИХ ГОРИЗОНТОВ МЕНИЛИТОВЫХ СЛОЕВ КАРПАТ

Резюме

Изученный лепидологический материал происходит из палеогеновых менилитовых слоев северо-восточной части флишевых Карпат, из района скольской единицы (фиг. 1). Присутствие различных экологических горизонтов: нижнего

батипелагического, неритическо-сублиторального и верхнего батипелагического установленное Ежманьской и Котлярчиком (1968) и Ежманьской (1968) обнаружило необходимость изучения чешуй Clupeidae в среде указанных выше горизонтов. В этой работе указаны результаты, касающеся только обоих батипелагических горизонтов.

Чешуи Clupeidae в большом количестве выступающие в менилитовых сланцах сохраняют оба слоя, которые строят чешуи современных рыб — гиалодентиновый слой и основную пластинку. Состояние сохраненных чешуй позволяет проследить все морфологические признаки, которые наблюдаются на чешуях современных сельдевых рыб. Чешуи карпатских Clupeidae характеризуются большим различием формы, положением бороздок и линией заднего края (пл. 58, 59), а некоторые из них имеют кроме того бугорки, которые заметны только на поверхности основной пластинки. На базе образцов с сохраненным чешуйным покровом и морфологического анализа отдельных чешуй, проведено реконструкцию чешуйного покрова *Clupea sardinites* Heckel и *Alosa* cf. *sagorensis* Steindachner. У третьего представителя, *Alosa* sp. возможна была только частичная реконструкция чешуйного покрова. В этих реконструкциях использовано кроме того некоторые закономерности в положении и структуре чешуй, наблюдаемые у современных Clupeidae, а также определено синонимы чешуй описанных до сих пор из Карпат.

У *Clupea sardinites* задний край чешуй ровный, бороздки отчётливо обозначаются на поверхности. Только у этого вида можно наблюдать изменения толщины чешуй в зависимости от возраста осадков. Индивидуа из нижнего батипелагического горизонта имеют толстые чешуи, зато в батипелагическом верхнем горизонте чешуи являются довольно тонкими.

Чешуи *Alosa* cf. *sagorensis*, которые строят плотный покров имеют вырезанный задний край, а на поверхности основной пластинки кроме бороздок выступают по-разному помещенные бугорки (фиг. 7). Присутствие характерной, асимметрической чешуи в области грудных плавников (фиг. 7*e*) указывает на существование у этого вида борозды, в которой находится первый луч грудных плавиков. Этот вид, до сих пор не отмеченный в менилитовых слоях, указано на основе анализа структуры чешуй и костей жаберной крыши.

Покров тела *Alosa* sp. составляют два типа чешуй, которые различаются между собой наличем или отсутствием бороздок в передней части (фиг. 9*a*, *b*). Это тонике чешуи, имеющие вырезанный задний край. Так же как у *Alosa* cf. *sagorensis* в чешуйном покрове выступали асимметрические чешуи (фиг. 9*c*), которые свидетельствуют о наличии борозды в области грудных плавников.

Видовое различие представителей Clupeidae в профиле менилитовых слоев дает возможность использования этих форм и их чешуй к стратиграфическим целям (таб. 2).

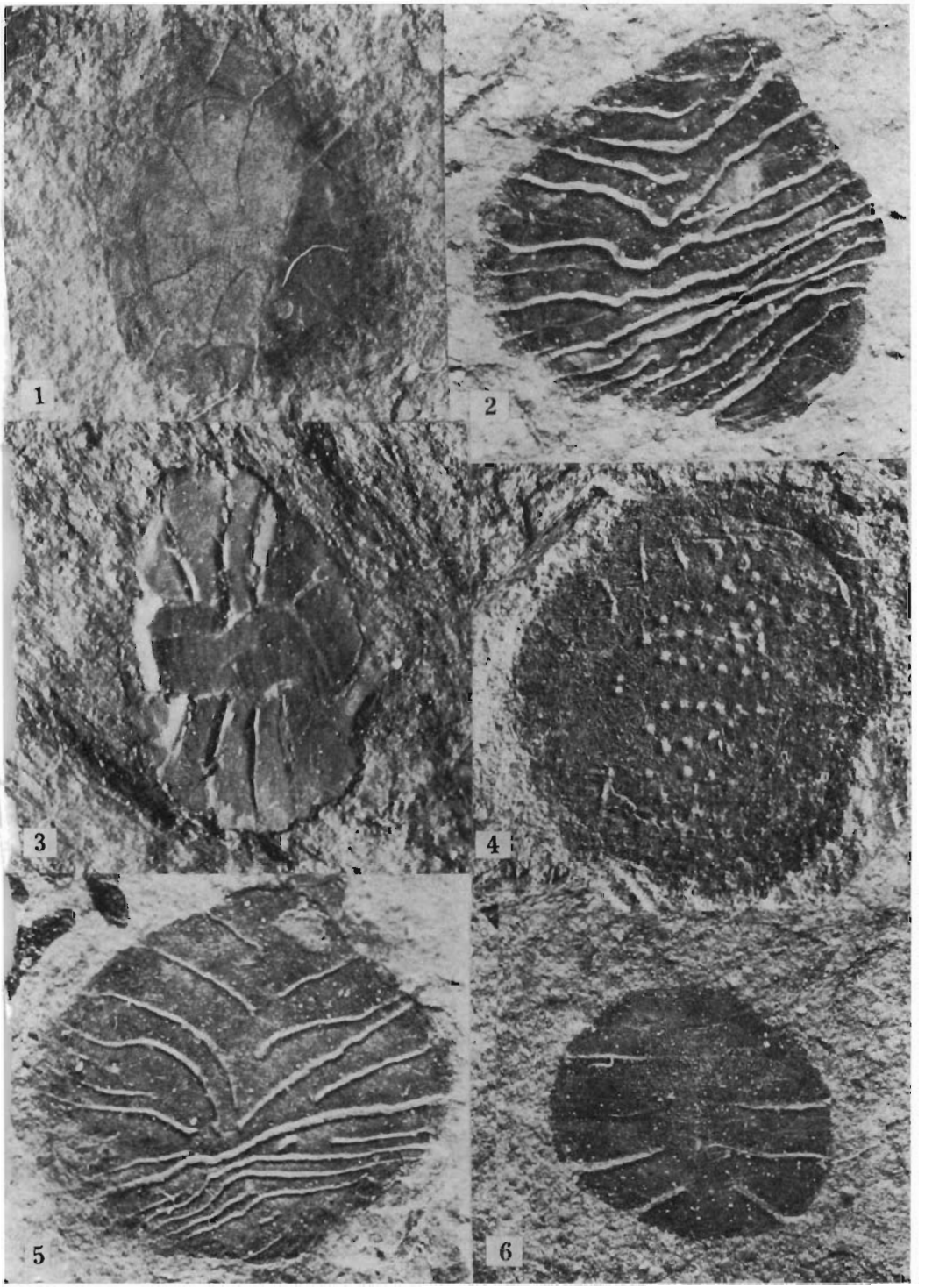
EXPLANATION OF PLATES 58 and 59

Plate 58

1. Hyalodentine layer of scale in *Clupea sardinites* Heckel (Z. Pal. Wr. Ł/43), × ca 13.
2. Lamellar layer of scale in *Clupea sardinites* Heckel (from a medial surface) (Z. Pal. Wr. Ł/57), × ca 12.
3. Notches on a underside surface of lamellar layer in *Clupea sardinites* Heckel (Z. Pal. Wr. Ł/2), × ca 9.
4. Nodules on the medial surface of lamellar layer in *Alosa* cf. *sagorensis* Steindachner (Z. Pal. Wr. Ł/1), × ca 9.
5. Scale in *Clupea sardinites* Heckel with vertical and horizontal grooves (Z. Pal. Wr. Ł/126), × ca 11.
6. Rounded scale in *Clupea sardinites* Heckel (Z. Pal. Wr. Ł/80), × ca 14.

Plate 59

1. Scale of Clupeidae with reticular pattern of grooves (Z. Pal. Wr. Ł/172), × ca 12.
2. Scale of *Alosa* sp. (Z. Pal. Wr. Ł/7), × ca 12.
3. Scale in *Alosa* cf. *sagorensis* Steindachner with crenellated posterior border (Z. Pal. Wr. Ł/4), × ca 10.
4. Operculum in *Alosa* cf. *sagorensis* Steindachner (Z. Pal. Wr. Ł/3), × ca 3.5.
5. Bones and scales of *Alosa* cf. *sagorensis* Steindachner (Z. Pal. Wr. Ł/3), × ca 0.8.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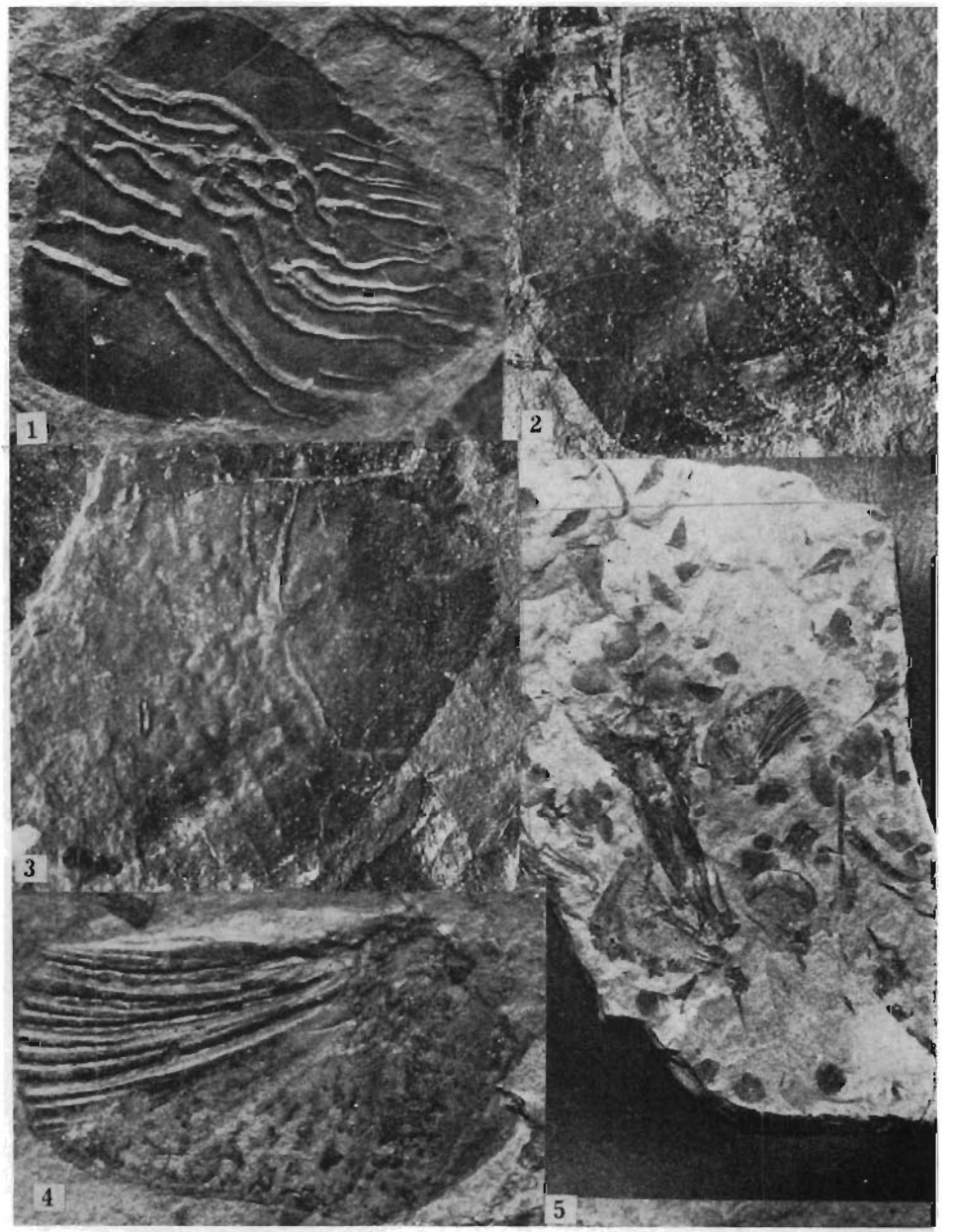
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