Ichthyoliths and deepening events in the Devonian carbonate platform of the Holy Cross Mountains

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Disarticulated fish microremains from the Middle Givetian to early Frasnian of the Holy Cross Mts include representatives of the most groups known from the Devonian: placoderms, elasmobranchs, holocephalians, acanthodians, osteichthyans (mostly osteolepidids) and actinopterygians. Taxonomic identifications are possible usually only in very general terms and only in two cases the generic level has been reached: *Phoebodus* among euselachians, and *Moythomasia* among paleoniscids. Many of these groups, regarded traditionally as typical dwellers of lacustrine to resticted marine nearshore biotopes, apparently flourished also in the offshore, open shelf carbonate (peri-reef) settings. The sequential replacement of the fish faunas was primarily influenced by eustatic events, in like manner to invertebrate communities.

Key words: ichthyoliths, paleoecology, Devonian, Poland.

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Introduction

Middle and Late Devonian fish remains from the Holy Cross Mountains were previously studied by Gorizdro-Kulczycka (1934, 1950) and Kulczycki (1957); their materials comprised chiefly macrofossils collected by Jan Czarnocki, particularly at Wietrznia and Kadzielnia quarries in Kielce. Isolated late Devonian shark teeth have been studied by Ginter (1990) and Ginter & Ivanov (1992) .

The material studied here was derived from conodont samples (Racki 1985, 1993; Racki & Bultynck in preparation) in several new localities. It consists of microscopic skeletal elements, chiefly isolated teeth and scales.

The main aim of the paper is a preliminary analysis of the ichthyoliths from the Givetian and early Frasnian of the western Holy Cross Mountains.

The senior author (J.L.) is responsible for taxonomic part; geological and stratigraphic data are provided by the junior author (G.R.), ecologic interpretations are joint.

The material elaborated is housed at the Department of Earth Sciences of Silesian University in Sosnowiec (abbreviated GIUS-4-412).

Material

Ichthyoliths are very subordinate skeletal components of the Middle and Late Devonian carbonates of the Holy Cross Mountains, but some bone-enriched levels were recognized in the course of conodont studies. The sections sampled are grouped in the western Holy Cross Mountains and represent both the Kostomłoty basin area, and the Kielce platform southern facies domain. The characteristic and stratigraphic setting of the 14 localities selected for this study are given in Racki (1993).

The ichthyolith collection studied (above 1000 specimens) consists of disarticulated, small skeletal elements recovered from acetic acid residues. The most common are single teeth but scales and miscellaneous bone fragments predominate in a few samples. Their typical sizes range from 1 to 4 mm, and biggest specimens do not exceed 9 mm. Most of specimens are broken and worn, which indicates some post-mortem transport and wear (evident in some cases e.g. at the Góra Zamkowa section, set C) and/or breaking of delicate elements during sample processing. Ferruginous encrustations occur commonly in the Laskowa locality.

The quantity of fish remains in the samples examined is strongly differentiated, ranging from a few specimens to several hundreds in two sites: Posłowice and Laskowa.

To date two different taxonomic procedures have been employed in ichthyolith studies: (1) a utilitarian approach based exclusively on morphological characters, with usage of a code system of letter and number descriptors, without implying any zoological relationships (Doyle *et al.* 1974; Tway 1979), and (2) the more natural zoological approach (Gross 1973; Karatajute-Talimaa 1978; Storrs 1987). The latter procedure is generally followed herein, although a part of the material remained indeterminate due to fragmentary preservation and/or lack of comparative collections. Most of vertebrate stocks known from the Devonian are recognized, ranging from placoderms to advanced bony fishes.

Placodermi

Numerous strongly disarticulated and broken, cellular bone scraps lacking specific diagnostic features are assignable only to the gnathostomates.

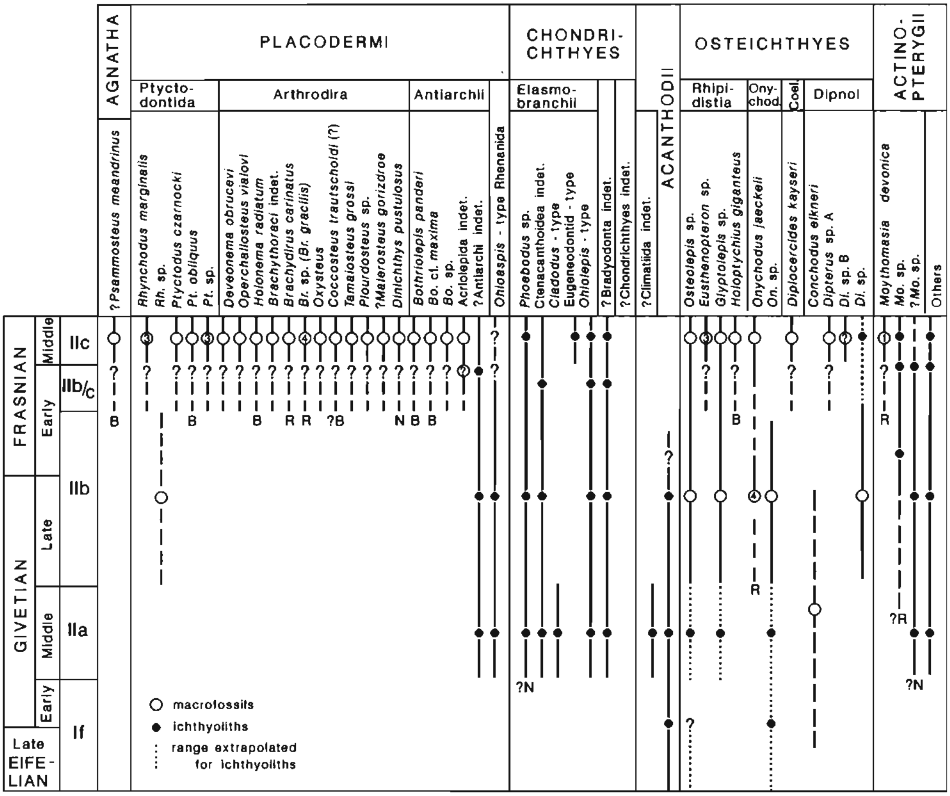

Fig. 1. Distribution of fish in the Givetian and Frasnian of the Holy Cross Mts based on macrofossils (data from Gorizdro-Kulczycka 1934, 1950; Kulczycki 1957) and ichthyoliths.

Occassionally, dermal bone fragments with a characteristic ornamentation can be found. The ornamentation consists of evenly spaced, hemispherical, rounded and smooth tubercles composed of the pallial dentine. The pattern of their distribution seems to be similar to the exoskeletal sculpture of different placoderms, especially antiarchs. The presence of placoderms in the Devonian limestones of the Holy Cross Mountains is well established as a result of previous studies of the macrofossils (Fig. 1), and new undescribed material collected by Tomasz Wrzołek at Góra Łgawa (set R, well-preserved specimen of *Bothriolepis*), Góra Zamkowa and Śluchowice (set A). In addition, varied rhenanid tesserae (Fig. 2A-B) were found in some samples; some are (cf. Gross 1973; Vieth-Schreiner 1983) of the *Ohioaspis*-type (Wells 1944).

Occurrence.– Middle Givetian to early Frasnian of Laskowa, Trzemoszna, Posłowice, Góra Zamkowa (sets A_2-I), Wietrznia I (set A_1), Jaźwica (set L), Wola Jachowa, Śluchowice, Górno (set C).

Problematic placoderm or chondrichthyan(?) scales.– In some samples there are unusual dermal denticles (Fig. 2C-E) with the 'base' very poorly developed as a narrow rim. The ventral surface is flat to strongly concave

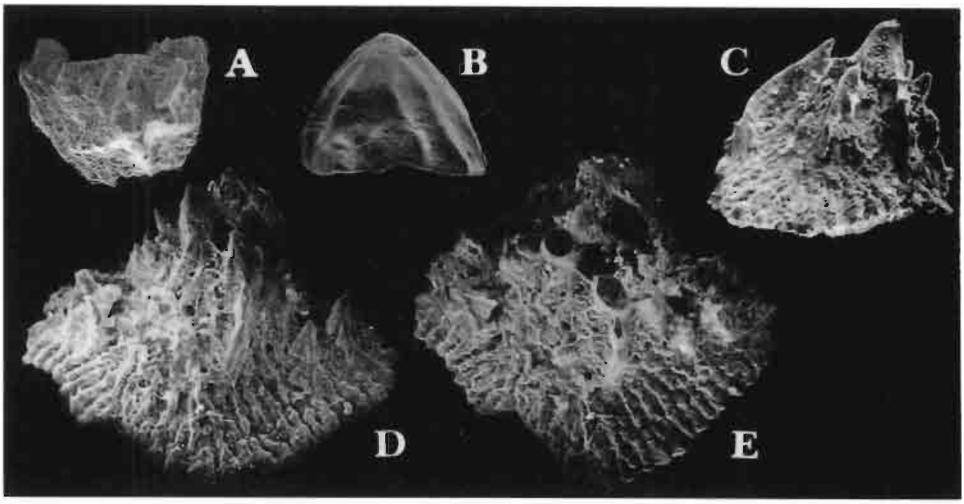

Fig. 2. Givetian placoderm (?rhenanid) tesserae of ?*Ohioaspis*-type (A-B) and problematic placoderm or chondrichthyan scales (C-E) in occlusal (A, E) and lateral (B-D) views. Laskowa (A), Wietrznia-I (set A_1; B) and Trzemoszna (C-E); × 40 (A) and × 25 (B-E).

conically. The crown is notably thin and formed by numerous, irregularly distributed, vertical or somewhat oblique thorns ('cusps') of different size. In lateral and dorsal views these specimens are comparable to mucuous membrane denticles of some xenacanthids (e.g. *Orthacanthus* and *Antarctilamma*; Zangerl 1981; Young 1982). On the other hand, these ichthyoliths may represent a peculiar tesserae variant of the placoderms (cf. Gross 1973) and buchanosteid-type body scales (S. Turner, letter communication 1992).

Chondrichthyes

Chondrichthyan remains are a significant component of the ichthyolith assemblages from some sites. Their notable diversity is rather surprising in contrast to the Devonian fish macrofossil data from the Holy Cross Mountains.

***Phoebodus* sp.** (Figs 3, 4M-N).– Above 60 teeth have been found. Their 1.2 to 4.5 mm in height with well developed diplodont-type crown, three to five cuspidate most characteristic features are two prominent, curved, lingually and outwardly diverging lateral cusps separated by one (in small teeth) or three (in larger specimens) smaller mesial cusps. The lateral cusps are rounded to oval in section, compressed mesio-distally, forming a cutting edge near the apices. The faces of the crown are smooth (Fig. 3A-C, F-H, J and Fig. 4N), although the labial face of the base may be striated in some specimens (Fig. 3E, I, L). No shiny enameloid-like layer has been observed on the crown and its cusps.

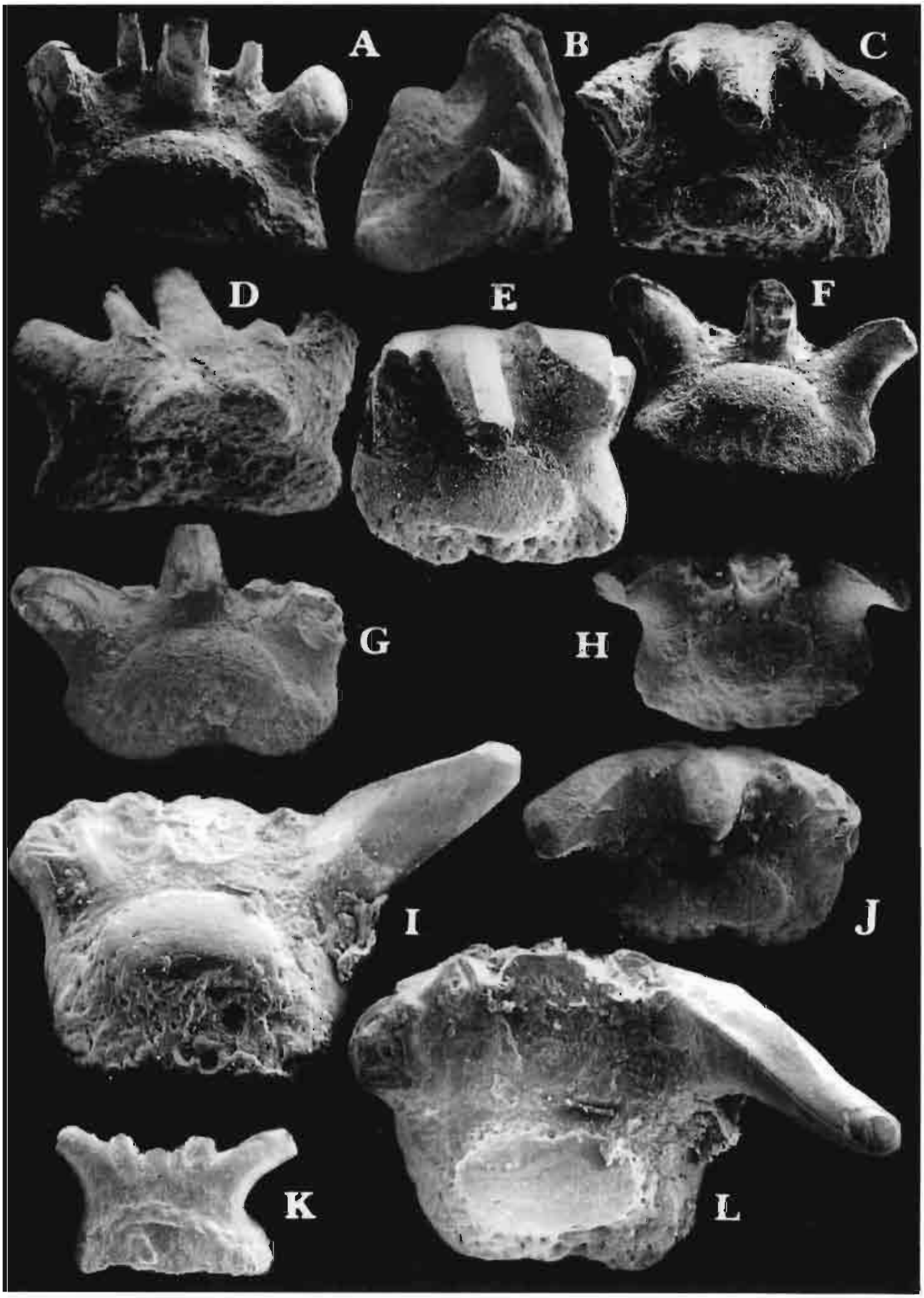

Fig. 3. *Phoebodus* sp., six differently preserved teeth in lingual (A, F-G, I), lateral (B), occlusal (C, E, I, L), and oblique, labio-basal (D, K) views; Givetian, Laskowa (A-H, J-K) and Posłowice (I, L); all × 25.

The root of the teeth is composed of a cancellous bone-like tissue. The vascularization is of the anaulacorhize-type with many entrant vascular foramina devoid any particular spatial organization. The root projects strongly lingward forming a prominent torus exhibiting a marked swelling on the dorsal surface. The basal face of the root is either flat (in smaller teeth) or concave (in larger ones), with the depression elongated mesio-distally and located more labially (cf. Fig. 3D).

The teeth examined strongly resemble specimens identified by Hussakof & Bryant (1918) as *Dittodus priscus* (Eastman 1902) and assigned to pleuracanth sharks. It is especially true for the more minute, three-cuspidate varieties. However, the larger specimens are morphologically very similar to the teeth classified in *Phoebodus* by Newberry (1889; see also Gross 1973). The teeth studied are thus attributed to this genus, and it is assumed that their morphological and size variability reflects either ontogenic heterodonty or mono- or di-gnathic heterodonty as discussed by Duffin & Ward (1983: pp. 105-106).

Two different species are possibly represented in the material under study differing mainly in the presence or absence of a striation on the labial face of the tooth crown.

Occurrence.– Middle Givetian of the Kostomłoty area (Laskowa; see Racki 1985: Pl. 6: 1), and Late Givetian (Posłowice) to ?Early Frasnian (?Wietrznia I, set C) of the Kielce Region.

Ctenacanthoid(?) dermal denticles (Fig. 4F-H, J-K).– Several tens of dermal denticles studied well correspond to compound scale type belonging to the crown-platform group (cf. ctenacanthoid morphotype of Reif 1978: pp. 111-112, Tab. 1) despite the fact that their crowns are not very thin and denticles as a whole appear rather robust. The dermal elements exhibit broad variations, but they are preliminarily referred to the ctenacanthoids only. These scales co-occur with teeth of *Phoebodus* in some sites and could be conspecific with them.

Occurrence.– Middle Givetian of the Kostomłoty area (Laskowa) and Late Givetian to Middle Frasnian of the Kielce Region (Trzemoszna, Posłowice, Kowala).

Cladodont teeth.– Several varied, mostly fragmentary cladodontiform teeth (Fig. 4E) from the Laskowa site are distinctly different from those determined as *Phoebodus* sp. by having their cusps approximately similar in height. The largest one attains 9 mm mesio-distally, and 5 mm labio-lingually (both measurements across the root). A distinct striation is visible on the basis of the crown in one specimen. Such teeth have traditionally been classified in the genus *Cladodus*, but the typical cusp pattern is actually common in the Cladoselachida, Symmoriida and Cten-

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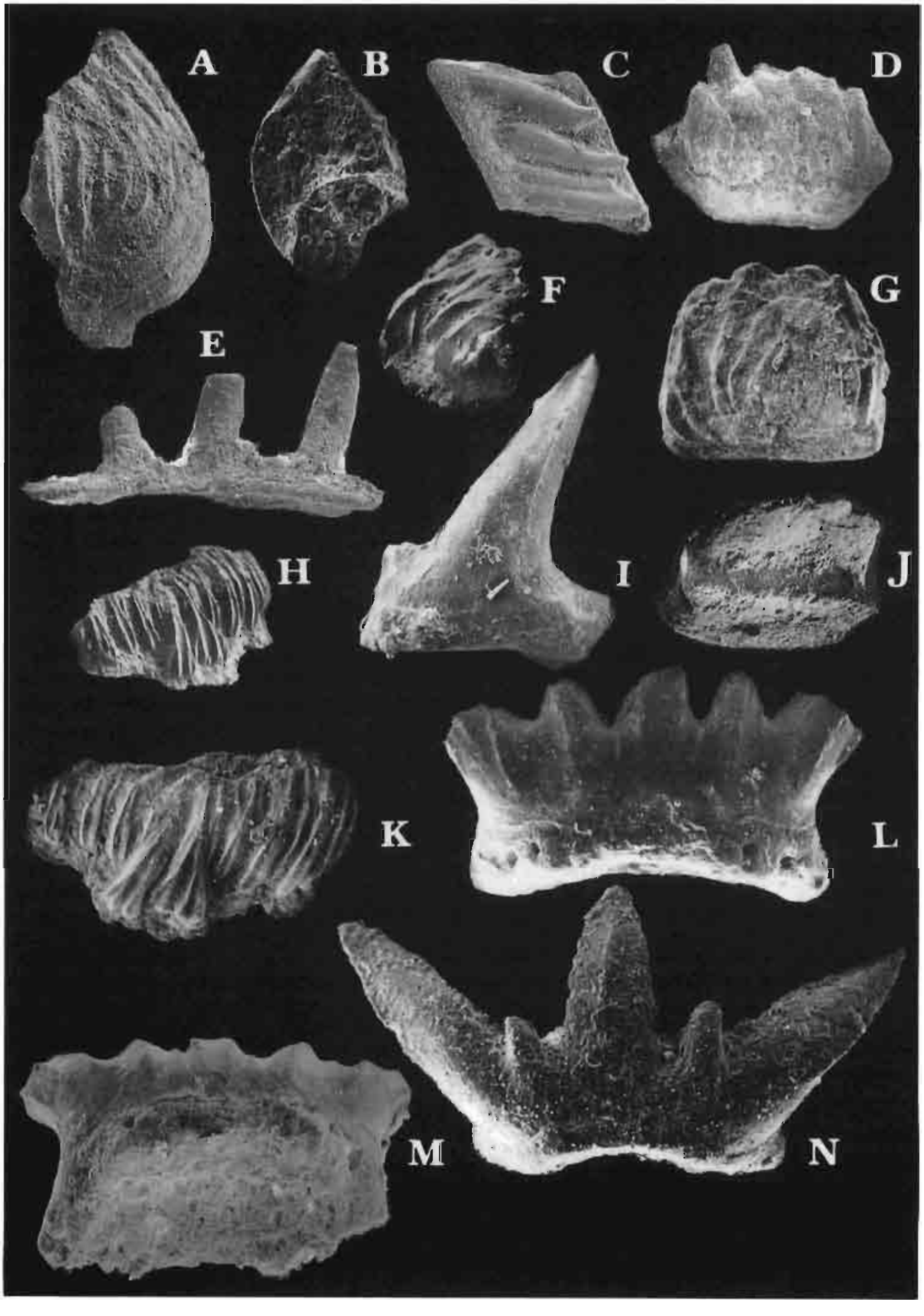
Fig. 4. Various elasmobranch remains from Givetian (A-B, D-K and N) and Frasnian (C, L-M). ❑A-B. *Protacrodus* or *Cladolepis*-type scales in occlusal (A) and labial (B) views; Laskowa; × 40. ❑C-D. Scale variants of morphogenus *Ohiolepis* in dorsal views; Czarnów (C) and Laskowa (D); × 40. ❑E. Cladoselachid tooth probably belonging to *Monocladodus* in lateral view; Laskowa; × 25. ❑F-H, J-K. Ctenacanthoid(?) compound dermal denticles in different



oblique lateral (F, J), occlusal (G, K), and anterior (H) views; Laskowa (F-G, J) and Posłowice (H, K); × 25 except for H that is × 20. I. Cladodont-type tooth in labial view; Laskowa; × 25. ❑L-N. *Phoebodus* sp.; 'cladodont' (L-M) and 'diplodont' (N), type teeth in labial (L, N) and basal (M) views; Kostomłoty (L-M) and Laskowa (N); × 50.

acanthida. In addition, one damaged specimen (Fig. 4F) is marked by a single prominent cusp and might represent cladoselachid *Monocladodus* tooth.

Eugeneodontid teeth.– A single Frasnian specimen (Fig. 5A-B) from Kowala displays a narrow crown with sharp but serrated occlusal crest, ridged and slightly expanded laterally on both labial and lingual faces. The length of the crown is about 5 times larger than the height. The base is slightly higher than the crown, concave and oblique to the crown axis. The tooth superficially resembles lateral teeth of the eugeneodontid *Gilliodus* from the Pennsylvanian of North America, particularly of *G. orvillei* Zangerl 1981.

?*Ohiolepis*-type scales.– Rare, highly specialized compound scales (Fig. 4C-D) are typified by a massive, bone-like basis and a very specific crown composed of several denticles curved posteriorly. The ventral surface of the basis is convex, like in acanthodian scales. The scales are of the *Protacrodus*-type (as defined by Reif 1978: pp. 114 and 127) and probably represent *Ohiolepis*. Our specimens differ from *O. frohnratensis* Friman 1983 in denticles being developed in the German species as simple thorns; *O. newberryi* Wells 1944 (see alsso Gross 1973; Friman 1983) diplays longitudinal grooves on the denticles. It seems more reasonable to determine them only (cf. Zangerl 1981) as dermal element of unidentified chondrichtyan. This is also true for specific micromeric scales (also of *Protacrodus*-type?) with a great basal canal and horn-like to three-cuspidate crown (Fig. 4A-B) sporadically occurring at Laskowa.

Occurrence.– Middle Givetian to Early Frasnian of the Kostomłoty area (Laskowa, Wola Jachowa, Czarnów) and Late Givetian to early Frasnian of the Kielce Region (Posłowice; Wietrznia-II, set C).

Undetermined 'bradyodont' teeth.– Some peculiar teeth show the crown composed of tubular dentine (*sensu* Zangerl 1981: p. 12), probably a synapomorphic feature of the 'bradyodont', paraselachid holocephalians of Lund (1986).

These numerous problematic teeth (Fig. 5I-P) are variable in shape which ranges from regularly quadratic and rectangular to rounded oval. The upper surface of the crown is either flat or slightly transversally convex and frequently exhibits several regularly distributed pits (Fig. 5K and O); the pores probably represent individual vascular channels exposed after wear of the vitrodentine layer. The crown overlaps the root. The crown/root junction is shaped as a neck canal with a row of relatively large foramina (Fig. 5P). The root surface is smooth or slightly concave, in some cases graben-like shaped. The root is strongly projecting downwards in form of a simple blade (Fig. 5L) in few specimens.

Fig. 5. Diversity of chondrichthyan remains from Givetian (C-L,and O-P) and Frasnian (A-B, and M-N). ❑A-B. Tooth possibly belonging to eugeneodontid genus *Gilliodus*, in lingual (A) and labial (B) views; Kowala; × 50. ❑C-H. Chondrichthyan cyclomorial scales (*Cladolepis gunnelli* Wells 1944) in dorsal (E-G), ventral (D, and H) and latero-anterior (C) views; Laskowa;

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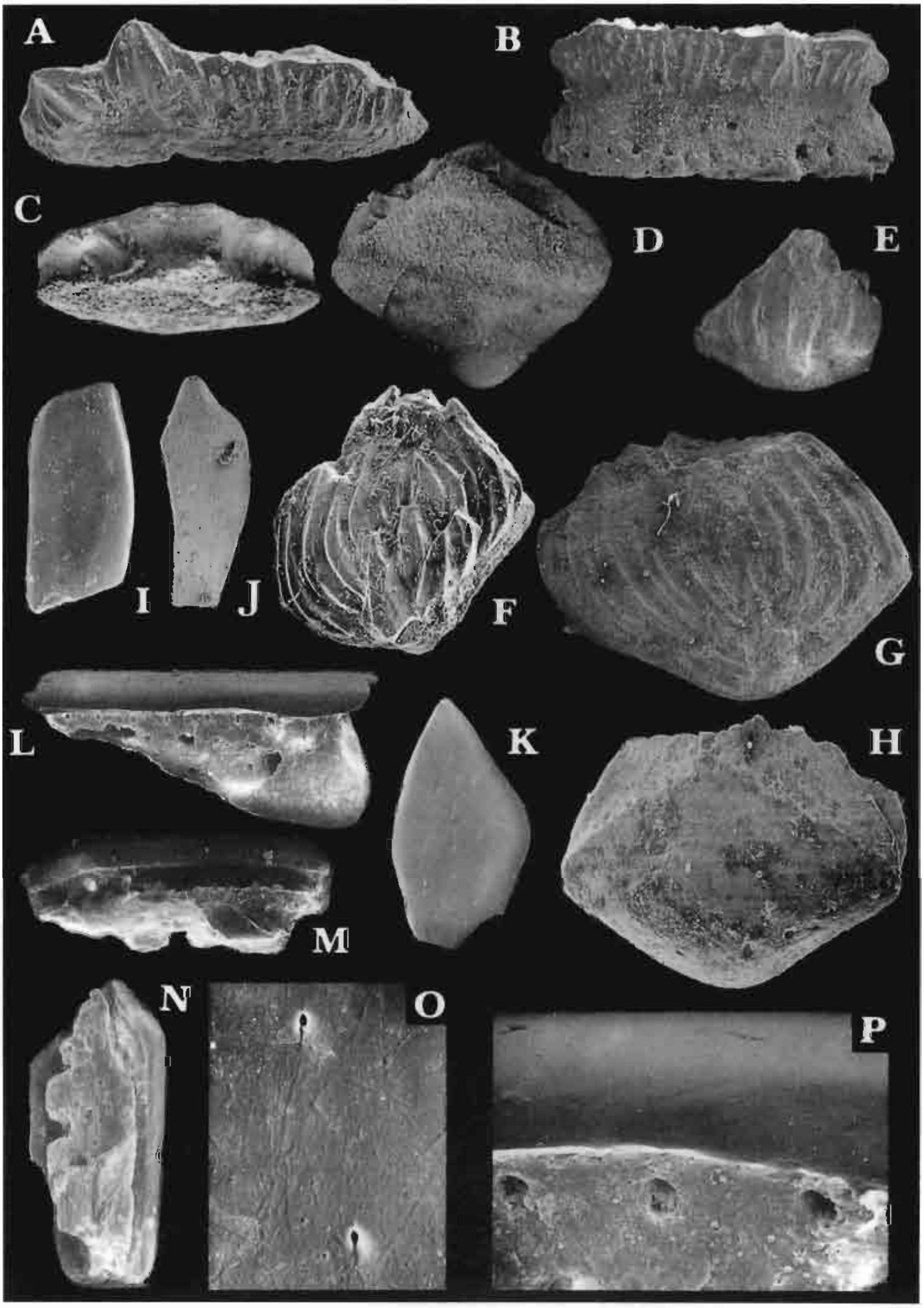

all × 25 except for F taken × 50. ❑I-P. Probable bradyodont teeth in occlusal (I-K), labial (N) and lateral (L-M) views, and details of pitted outer coronal layer (O) and neck canal (P); Posłowice (I; L, magnified in P), Góra Zamkowa (set A_2; J), Jaźwica (set B; K, magnified in O) and Wola Jachowa (M-N); all × 40 except for O (× 300) and P (× 150).

Occurrence.– Middle Givetian to early Frasnian of the Kostomłoty area (Laskowa; Wola Jachowa; Górno, set C) and Late Givetian to Middle Frasnian of the Kielce Region (Marzysz, Posłowice, Jaźwica, Góra Zamkowa, Wietrznia-I).

Undetermined chondrichthyan(?) scales.– Some compound scales, known only from Laskowa, are distinguished by a thick, concave bone base resembling that of the ctenacanthoid dermal denticles (Fig. 5C-H). However, their crowns consist of many strongly differentiated ridges (odontodes). The few first (embryonic) are relatively massive and short, the second-ring odontodes are numerous, slightly longer and thinner, and those of the later rings are also numerous, but delicate and sharp. Externally, the cyclomorial scales are identical to the dermal elements of some 'cladodontids' and 'bradyodonts', and may be referred to *Cladolepis* (Wells 1944; Gross 1973).

Occurence.– Middle Givetian of the Kostomłoty area (Laskowa) and Late Givetian to early Frasnian of the Kielce Region (Trzemoszna; Wietrznia, sets ?B and C).

Acanthodii

Acanthodian remains are markedly limited to samples from the Middle Devonian strata where ichthyolith association consists almost exclusively of dermal scales. Additionally, one small-sized tooth, ca. 1.8 mm long, from Laskowa superficially resembles those of diplodont shark teeth, but is distinguished by the lack of any histological differences between the root and crown; both parts are composed only of dentinous tissue. It is proposed that the specimen derived from a climatiid acanthodian possessing dentigerous jawbones. Another large-sized element (Fig. 6G) from this site is considered as a problematic fragmentary acanthodian jaw.

Acanthodian scales.– Several tens of dermal scales are small-sized, mostly less than 1 mm in length, maximally up to 2.5 mm. Most of them possess a diamond- or rhomb-shaped crown, and a bulbous (rarely flat) base separated from the crown by a more or less marked constriction (neck). The base is devoid of any basal canals and composed of an acellular bone like tissue, whereas the crown is built of true dentine; the scales lack an enameloid-like surface (Fig. 6A-F). These last features are diagnostic synapomorphies of all acanthodians (Maisey 1986: p. 229).

The surface of the crown in most scales is mainly smooth and without pore canals; these scales are assignable (e.g. Wells 1944; Storrs 1987) to *Acanthoides? dublinensis* Stauffer 1938. In some specimens anterior ribbing is visible or the crown hangs over the base in form of a serrated blade, and these are presumably *Cheiracanthoides comptus* Wells 1944 (cf. Gross 1973). Similar scale assemblages are frequently reported from various Devonian strata (Vieth-Schreiner 1983; Blieck *et al.* 1988: Fig. 3).

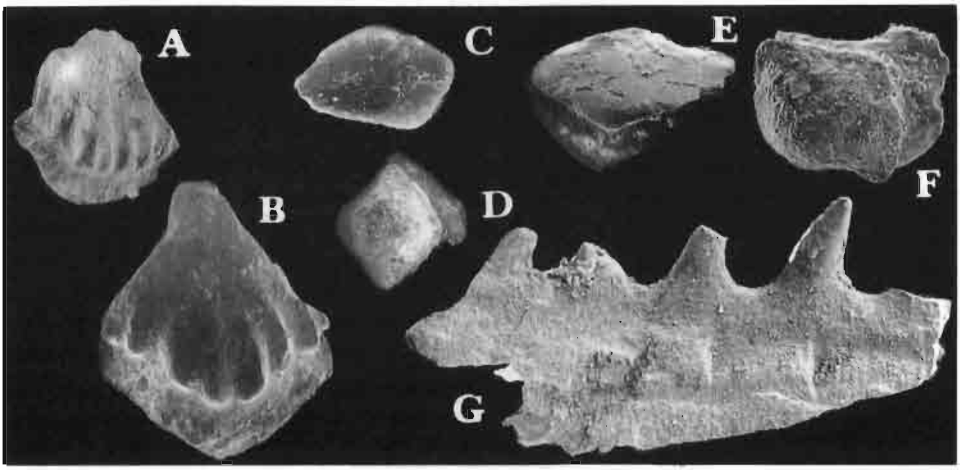

Fig. 6. Middle Devonian acanthodian scales (A-B – *Cheiracanthoides comptus* Wells 1944; C-F – ?*Acanthoides dublinensis* Stauffer 1938) and fragment of jaw(?) (G). Dorsal (A-C), ventral (D,-F), lateral (E, H), and oblique-dorsal (F) views. Laskowa (A, D-G), Skały (B) and Wietrznia-I (set A_1; C); all × 40 except B, E-F (× 50) and G (× 25).

Histologic analysis of the Holy Cross Mountains material will need to be performed before more detailed determination is possible.

Occurrence.– Latest Eifelian through Givetian of the Łysogóry Region (Skały), Kostomłoty area (Laskowa), and Late Givetian of the Kielce platform (Trzemoszna, Posłowice, Wietrznia).

Osteichthyes

Skeletal elements of the bony fish (non-cycloid scales, teeth and various bone fragments) are the most abundant and widespread ichthyoliths studied. They are determined here only to family level (cf. Jarvik 1948: p. 5, and 1950: p. 13; Vorobyeva 1977). Two distinct morphological groups, both scales and teeth, are distinguished herein which apparently (cf. Schultze 1969, 1977; Vorobyeva 1977) represent distinct evolutionary branches within the rhipidistians.

An incomplete, large (nearly 1 cm long), thin cycloid scale from Czarnów may belong to a coelacanth. The same affinity is probable for exoskeletal fragments with tubercular ornamentation (Fig. 7H) found at Śluchowice.

Primitive osteolepidid remains.– Scales (Morphotype A) (Fig. 7A, E-F), found in most of the localities, are variable in size (mostly 2-3 mm, the biggest specimen attaining 9 mm in length), and shape, with the non-overlapping part covered with a smooth, shiny layer of cosmine. The external surface of the scales is without any ornamentation, with exception of a finely pustulose pattern observed in some specimens. The non-overlapping and overlapping parts are delineated by distinct grooves. The visceral surface shows an inner ridge, pit and process.

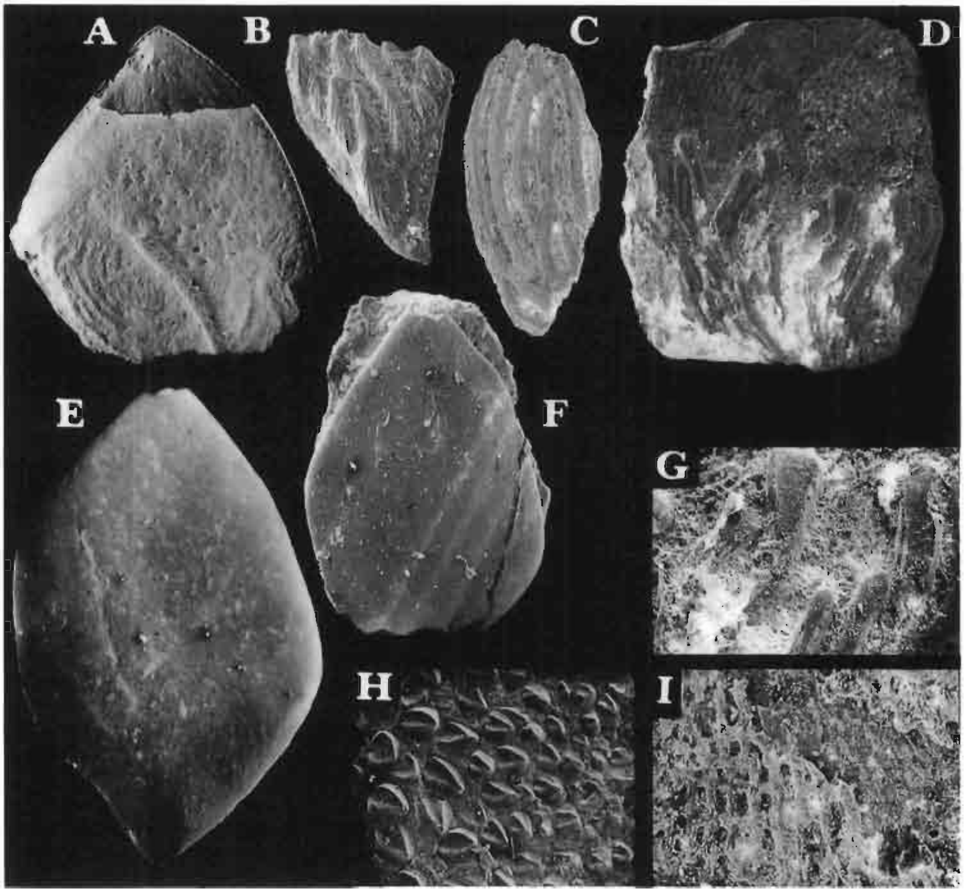

Fig. 7. Rhipidistian scales (A-G, I) and sculptured exoskeleton (H), Givetian (A, C-G, I) and Frasnian (B, H). ❑A, E-F. Primitive osteolepidid scales (Morphotype A) in ventral (A, partly broken) and dorsal (E-F) views; Posłowice, × 10. ❑B-D, G, I. Avanced osteolepidid and/or porolepidid scales (Morphotype B) in dorsal views (B-D) and details of their ornament (G, I); Śluchowice (B) and Wietrznia-I (set B; C, D magnified in G and I); × 25 except for G (× 50) and I (× 100). ❑H. Coelacanth(?) exoskeletal fragment with a tubercular ornamentation; Śluchowice, × 50.

Similar scales are known from several primitive genera of the Osteolepididae, such as *Osteolepis* cited from Wietrznia by Gorizdro-Kulczycka (1950: p. 74), *Thursius*, *Latvius* and *Gyroptychius* (see Jarvik 1948, 1950; Vorobyeva 1977). The variety displaying finely pustulose ornamentation is strictly comparable with scales referred to *Gyroptychius* by Young & Gorter (1981).

Fang-teeth (Morphotype A) are small, conical to slightly curved (Fig. 8G). They are circular to oval in cross section, smooth or finely striated only near the base, and with a large great pulp cavity. The tooth apices lack any enameloid-like, shiny cups. Microstructure of all these teeth is polyplocodontid, typical of primitive osteolepidids including the genera listed above.

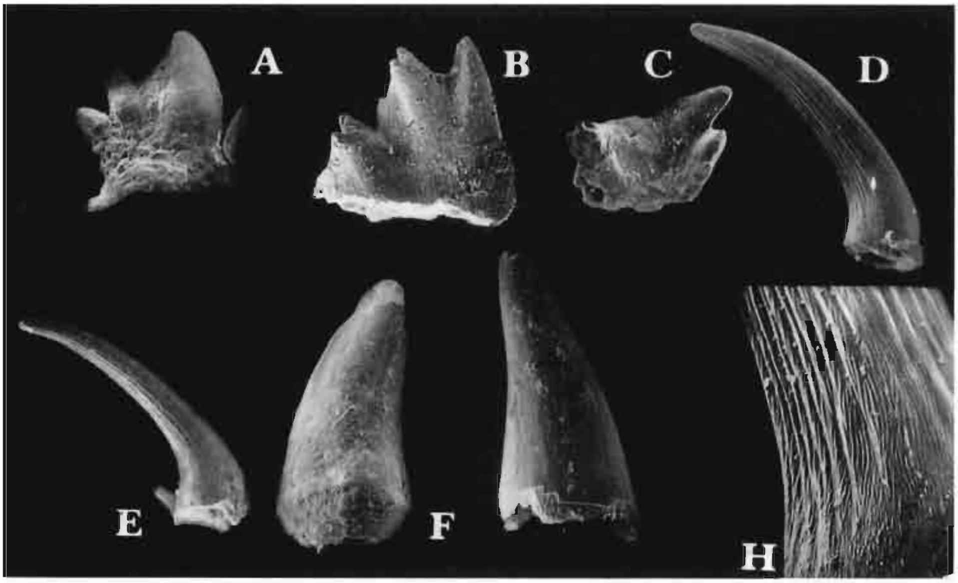

Fig. 8. Osteichthyan teeth, Givetian (C, E-G) and Frasnian (A-B, D, H). ❑A-C. Different dipnoan teeth in lateral (A-B) and oblique-labial (C) views; Jaźwica (set L; A), Kadzielnia (B) and Posłowice (C). ❑D-E and H. Ribbed, advanced rhipidistian teeth (Morphotype B); Wietrznia-I (set C; D, magnified in H) and Posłowice (E). ❑F. Onychodontid fang; Posłowice. ❑G. Smooth, fang tooth (Morphotype A) of a primitive osteolepid; Posłowice. All × 25 except for H (× 100).

Occurrence.– Middle Givetian to early Frasnian of the both regions (almost all sites), and possibly the latest Eifelian of the Łysogóry Region (Skały).

Advanced osteolepidid, and porolepidid scales.– This rare variety can be distinguished by its rounded-rhomboidal outline and non-overlap area covered with an ornamented cosmine layer (Fig. 7B-D, G, I). The sculpture is expressed as pronounced longitudinal ridges and/or grooves. Large pores are sometimes visible within the grooves, as well as fine peripheral ridges or flutes at the junction of the overlapping and non-overlapping parts. This group of scales may represent progressive osteolepidids and/or porolepidids, e.g. *Glyptolepis* and *Holoptychius* listed by Gorizdro-Kulczycka (1950: pp. 74-75).

Occurrence.– Middle Givetian to Early Frasnian of the Kostomłoty area (Laskowa, Wola Jachowa, Górno, Śluchowice) and Late Givetian of the Kielce Region (Marzysz; Posłowice; Góra Zamkowa; Wietrznia-I, set B).

Undeterminated rhipidistian teeth.– The teeth (Fig. 8D-E and H) are most common in almost all samples examined and characterized by slightly larger sizes than those described above (up to 12 mm), more or less pronounced ribbing, and commom S-curved appearance. Some of them probably have got eustenodontid microstructure, i.e. the outer enameloid layer seems to be strongly infolded which results in reduced or even no pulp cavity. Such teeth occur in different rhipidistians, although the kind of microstructure points to the advanced osteolepids and/or porolepids in some cases.

Onychodontid teeth.– Several more robust fangs are marked by fine stration in posterior part only. They, as well as their pulp cavities, are circular to oval in cross section (Fig. 8F). The teeth resemble specimens determined as *Onychodus* sp. by Vieth-Schreiner (1983) and Lelievre *et al.* (1988); the genus was already quoted by Gorizdro-Kulczycka (1950).

Occurrence.– Latest Eifelian through Givetian of the Łysogóry-Kostomłoty domain (Skały, Laskowa, Górno), Late Givetian to Middle Frasnian of the Kielce Region (?Trzemoszna; Posłowice; Marzysz; Góra Zamkowa; Jaźwica; Wietrznia, sets A-B).

Dipnoan teeth.– Small and damaged specimens (Fig. 8A-C) possibly correspond to teeth from different parts of the dipnoan jaw. There are three intergrown complex teeth, flattened or gently curved, placed on a solid base. A tooth from the Jaźwica site is marked by oblique orientation of separate cnops in relation to the wider basal part.

Occurrence.– Late Givetian to Middle Frasnian of the Kielce Region (Posłowice; Kadzielnia; Jaźwica, set L).

Actinopterygii

Paleoniscoid remains are rather common in several samples examined and include numerous flank scales, as well as infrequent teeth (Fig. 9A) of small size below 1 mm, conical shape and minute, translucent acrodine cap. Only the scales are described below in details.

***Moythomasia* sp.** (Fig. 9B, D-E, J-K).– Twenty five differently preserved scales have been found. They are rhomboidal, small-sized and bear a ribbed external surface and spiked posterior margins. A large articulatory peg and a prominent anterior articulatory facet is developed, as well as a thick isopedin base and a shiny, transparent ganoine crown. The ribs or ridges run horizontally, nearly parallel to the dorsal and ventral margins. Individual punctae, arranged in single rows between ribs, are visible in some specimens.

The scales examined are similar to those in species of *Moythomasia*, in particular *M. striata* Gross 1933 from the Rhenish Frasnian (see Jessen 1968). Any more accurate species determination is ambigue because of wide extent of scale variability within particular fish skeletons (Jessen 1968; Storrs 1987: pp. 367-368).

Occurrence.– ?Late Givetian of the Kielce Region (?Posłowice) and early Frasnian of the whole area (Wietrznia-I, Jaźwica, Górno, Wola Jachowa).

***Moythomasia*(?) sp.** (Fig. 9F-G).– Above 45 mainly broken scales have been collected.

This variant of paleoniscoid scales shows similar ornamentation pattern as those assigned to *Moythomasia* sp., but the ribs are deflected dorsally and upturned anteriorly; also the articular facet of the scales is

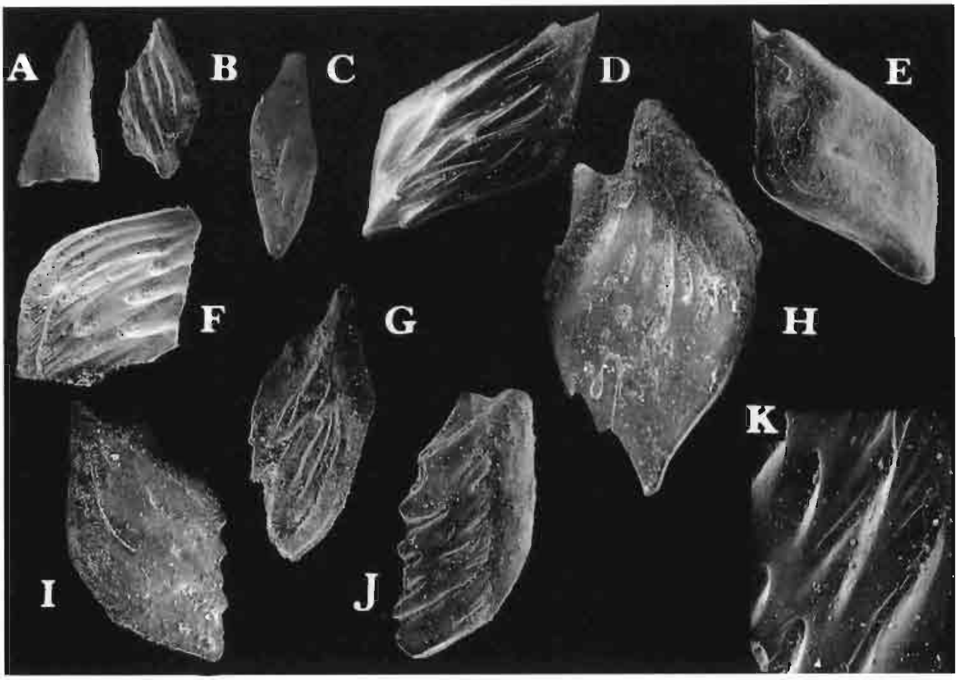

Fig. 9. Paleoniscoid ichthyoliths from Givetian (A, and G-J) and Frasnian (C-F, and K). ⅃A. Tooth in lateral view; Górno (set A); × 50. ❑B-K. Varieties of flank scales: *Moythomasia* sp. (B, D-E, J-K), *Moythomasia*(?) sp. (F-G) and undetermined paleoniscoids (C, H-I); Wietrznia-II (set C; B), Posłowice (C), Górno (set C, D-F; set A, G), Laskowa (H-I) and Jaźwica (set L; J magnified in K),. Ventral (B-D, F-J; details of sculpture in K) and dorsal (E) views; note variable dorsal articulary peg and articulary facet. All × 25 except for K that is × 90.

chiefly narrowed. These characters suggest strict affinities to scales described by Storrs (1987) from the Givetian to Frasnian strata of Iowa.

Occurrence.– Middle Givetian to early Frasnian of the Kostomłoty area (Laskowa, Górno, Czarnów) and Late Givetian of the Kielce Region (Posłowice, Wietrznia).

Other paleoniscoid scales.– Several other varieties of scales (Fig. 9C, H-I), probably representing in part Stegotrachelidae (e.g. Lelievre *et al.* 1988), occur within the material studied. Some specimens have ribs running diagonally (i.e. anterodorsally-posteroventrally). Other scales show a convex base and incipient ribbing developed exclusively in the posterior part.

Occurrence.– Middle Givetian to early Frasnian (Laskowa; Posłowice; Górno; Jaźwica; Wietrznia, sets A-B).

Distribution of the microvertebrate faunas

Remarkably, within the Holy Cross Mountains microvertebrate faunas, there are examples of possibly relic (Kulczycki 1957: pp. 354-356) and may be neo-endemic (eugeneodontids, ?bradyodont) occurrences, confirming

(Racki 1988: p. 127) a special biogeographic position of this part of the Laurasian shelf.

The recent biostratigraphic studies (Szulczewski 1971; Racki & Bultynck in preparation) allow refinement of the ranges of fish species in the Holy Cross Mountains (Fig. 1). The Frasnian association comprises elements of coeval ichthyofaunas of the Baltic region, e.g. the Lower and Middle Frasnian ichthyofaunas of the Snetnaja Gora through Daugava horizons of Latvia (see Lyarskaya 1978; Blieck *et al.* 1988).

Preliminary comparison of ichthyoliths studied with those from stratigraphically younger late Frasnian to early Famennian localities, in particular Kostomłoty, Kowala, Psie Górki, Kadzielnia, Domaszewice, Tudorów, Góra Łgawa and Grabina, point to a faunal replacement. The changes are expressed in a lowered frequency of osteolepidids, especially the primitive families, combined with higher contribution of the paleoniscoids, and in the appearance of many biogeographically new euselachians (e.g. *Monocladodus*, *?Ctenacanthus*; unknown earlier species of Phoebodus, Fig. 3L-M; see also Kulczycki 1957; Ginter 1990) and 'bradyodonts' (like Orodus, ?Petalodontidae); placoderm remains are abundant in some samples.

Environmental interpretations concerning Paleozoic fish have traditionally been based on findings from the Old Red Continent, particularly Canada, Scotland, Spitzbergen, Main and Central Devonian Fields of the Russian Platform (see Storrs 1987). Consequently, freshwater to brackish-lagoonal nearshore biotopes were previously assumed for such groups as the ostracoderms (e.g. psammosteids), placoderms, especially Brachythoraci, Ptyctodontida and Antiarchi, most of the acanthodians, osteolepid rhipidistians and dipnoans.

Representatives of the above mentioned groups have been found in the Givetian and Frasnian of the Holy Cross Mountains, either as macrofossils (Fig. 1) or as microremains. Their presence was used as an indication for strong continental, freshwater to lagoonal influences by Gorizdro-Kulczycka (1950: pp. 53, 75, and 78). Such an interpretation is, however, in clear contradiction to the conclusions derived from facies analysis: the abundance of diverse, strictly marine invertebrates in the bone-bearing deposits evidences an open shelf environment of normal marine salinity (for details see Szulczewski 1971 for the Wietrznia locality, Racki *et al.* 1985 for the Laskowa site). Only locally is it possible to accept possible episodic lowerings of salinity, e.g. in the case of charophyte-populated parts of the shallow, semi-closed basin (at Posłowice; Racki & Racka 1981) or strong influences of back-reef, restricted lagoons. A normal marine setting is also supported (cf. Wells 1944; Gross 1973; Storrs 1987) by the significant frequency of ctenacanthoid sharks, especially of the genus *Phoebodus*, and paleoniscoids of the family Moythomasiidae.

Revision of the commonly accepted ideas on strict hyposalinity was suggested already by Kulczycki (1957: p. 353) for the widespread Ptyctodontidae and *Dinichthys pustulosus* Eastman 1897. For the osteolepids this was proposed by Thomson (1969), who pointed out that they were primarily associated with proximal marine biotopes. The same is true also for other fish groups. They evidently inhabited offshore, carbonate shelf environments (see also Blieck *et al.* 1988) including peri-reef settings, but not extensive restricted-lagoonal domains. Lyarskaya's (1978: p. 70) conclusion that fish faunas from the marine carbonates are very scarce in comparison to those from clastic sediments seems questionable in the light of new data. There is no evidence of any reduced size range and/or dominance of one age class (for instance juveniles) in the studied material. Therefore, even an extensive seasonal migration of the fresh-water species toward more marine biotopes (see Schultze 1985 and Zidek 1988 for discussion) seems improbable in this case. Rather, these were euryhaline (cf. Novitskaya *et al.* 1983) fish, comprising amphidromous species freely moving between differing waters without the purpose of breeding.

Most of the 'continental'-type fish groups are known from marine transgressive levels in the Middle and Late Devonian of the East European Platform (e.g. Gross 1933; Obruchev 1958; Obrucheva & Obrucheva 1977; Lyarskaja 1978). The same pattern of distribution is seen in the western Holy Cross Mountains, where several significant facies and biological events, controlled primarily by eustatic fluctuations (cf. T-R cycles of Johnson *et al.* 1985), were established recently by Narkiewicz (1988) and Racki (1988, 1990).

Summarizing all available data on the Holy Cross Mountains ichthyofaunas, the following succession of bio-events can be tentatively proposed:

(1) A large mid-Givetian deepening pulse (base of T-R Cycle IIa) probably resulted in colonization of the Kielce Region carbonate bank by diverse benthic communities (cf. Racki 1988, 1993). It is also recorded in expansion of an open-marine fish association to the Kostomłoty area. Biogeographic mixing of the Rhenish-North American and Baltic-Russian elements (Gorizdro-Kulczycka 1950: p. 74) seems to be present already at this stage of the fish succession.

(2) The late Givetian (IIb) transgressive pulse initiated a temporary thriving of low-diversity rhipidistian-dominated associations in open shelf habitats of the temporary drowned stromatoporoid-coral platform. This was mainly achieved by a southward expansion of the Kostomłoty-type association which has been already demonstrated for invertebrate communities (Racki *et al.* 1985). Possible larger scale biogeographic changes are expressed by the entry of new dipnoan and placoderm genera (*Dipterus, Dinichthys*). As a rule, regressive interphases following the deepewning events, were associated with impoverishing or at most stabilisation of the fish biotas.

(3) The early Frasnian two step flooding (IIc) was connected with the acme of placoderm-dominated fore-reef faunas in the northern part of the Kielce Region, with notable contribution of ostracoderms and dipnoans of chiefly Baltic-Russian affinity (Gorizdro-Kulczycka 1950: p. 75). On the

regional scale, however, more important seems to be the development of paleoniscoid-dominated associations.

(4) Very important late Frasnian (regressive-) transgressive (IId; Narkiewicz 1988) events are presumed to be the main cause of the disappearance of Baltic-Russian affinities evidenced by macrofossil studies, and the rebuilding of the ichthyolith assemblages. The flourishing of many new, chiefly North Atlantic-Rhenish species, reflects a progressive evolutionary and ecologic replacements within the changing environments of the submerging Dyminy reef. On the other hand, these ichthyofaunas seem not to be much affected by the latest Frasnian rapid sea level changes and consequent 'mass' extinction. Diverse euselachian, sarcopterygian, and placoderm associations occur in the basal Famennian deposits (see Racki 1990). A biotic recovery, that culminated in the *Palmatolepis crepida* Zone, is also possibly manifested in fish diversification.

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Streszczenie

Zróżnicowane ichtiolity z pogranicza żywetu i franu Gór Świętokrzyskich obejmują przedstawicieli większości grup ryb znanych z dewonu takich jak plakodermy, żarłacze (m.in. rodzaj *Phoebodus*), zrosłogłowe, akantody, kostnoszkieletowe (głównie pospolite osteolepidy) i promieniopłetwe (w tym rodzaj *Moythomasia*). Dane z analizy ichtiolitów w znaczny sposób rozszerzają wyniki poprzednich badań opartych o makroskamieniałości i dokumentują wyraźne zmiany ewolucyjne (głównie wśród rekinów i paleoniscoidów) oraz ekologiczno-biogeograficzne w ciągu żywetu i franu.

Wiele grup kręgowców, uważanych uprzednio za typowe dla biotopów słodkowodnych i lagunowych, zasiedlało również pełnomorskie środowiska otwartego szelfu, w tym te ściśle związane z rafami. Sukcesja asocjacji ryb była w dużej mierze kontrolowana przez fluktuacje eustatyczne w sposób zbliżony do rozpoznanego dla biocenoz bezkręgowców, tzn. epizody transgresywne były okazją do dużych migracji i zmian biogeograficznych, a interfazy regresywne – okresami stabilizacji bądź ubożenia fauny ryb.