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Rhaetian fish remains from the Tatra Mountains

ABSTRACT: The fish remains extracted from bone beds occurring in the subtatric Rhaetian of the Mt. Hradok and Lejowa Valley sections in the Tatra Mountains are briefly described. The fauna comprises well established Rhaetian shark and actinopterygian genera. It is concluded that the vertebrate remains from Mt. Hradok are primary components of the sediments in which they have been found. The Lejowa Valley bone bed appears to contain both primary and prefossilised vertebrate remains.

INTRODUCTION

Rhaetian fish remains were previously reported from the Tatra Mts by Gaździcki (1974; Pl. 51, Figs 9—13). They were found in the sections of sub-tatric Rhaetian from the Juráňova and Lejowa Valleys, Mt. Mała Świnica, Mt. Mały Kopieniec, Mt. Wołoszyn, Szeroka Bielska Pass, Mt. Palenica Lendacka and Mt. Hradok. Fish remains are subordinate components of these deposits, being represented by relatively uncommon, scattered single teeth and scales. They are most common in organodetrital limestones, and especially in brachiopod-pelecypod biomicrites and biopelsparudites. The distribution of fish remains was shown on analytical sections by Gaździcki (1974, Figs 1, 3—5 and 8—9).

The bulk of fish remains discussed here are derived from two localities where they form bone beds. These bone beds were not however located *in situ*, but fragments of the lithology were found in the scree at the base of the Lejowa Valley and Mt. Hradok, sections (Fig. 1). The bone beds at the sampling places may be characterized as fish-pelecypod biosparites (in the case of Lejowa Valley) or biointramicrites composed of fish-brachiopod-gastropod and crinoid debris as well as intraclasts (Mt. Hradok).

The investigated fish remains were derived from the sequences which correspond both to the Lower and Upper Rhaetian of the Tatra Mts (see Gaździcki 1974a, b; Gaździcki & Iwanow 1976). It should be also noted that teeth of the genus *Acrodus* were previously reported from the "Gresten" Beds cropping out at Mt. Mały Kopieniec by Goetel (1917).

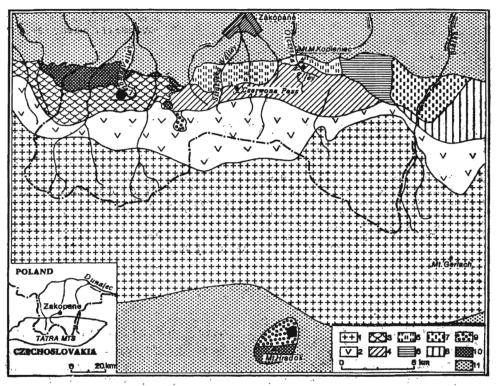


Fig. 1. Tectonic sketch of the Tatra Mts to show the location of the Rhaetian sections with fish bone bed (thick dots)

Tectonic units: 1 — crystalline core of the Tatra Mts; 2 — high-tatric series; 3—6 — subtatric (Križna) series: 3 Bobrowiec unit, 4 Suchy Wierch unit, 5 Mała Świnica unit, 6 Kopy Soltysie unit, 7 Skałki (Gęsia Szyja) unit, 8 Havran unit, 9 undivided series; 10 — sub-tatric (Choč) series; 11 — inner Carpathian flysch

This is the first study of fish remains from the Rhaetian of the Tatra Mts; it also contributes to the knowledge of fish remains from the Triassic of Poland (cf. Roemer 1870, Schmidt 1928, Liszkowski 1973).

C, J. Duffin is responsible for paleontological determination and descriptions of the fish remains, whereas A. Gaździcki for locational, stratigraphic and sedimentological data. Both authors share the responsibility for discussion and conclusions.

The material described in this paper is housed in the Institute of Paleobiology (formerly Institute of Paleozoology) of the Polish Academy of Sciences in Warsaw (abbr. ZPAL PI/1-117).

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SYSTEMATIC DESCRIPTION

The outline classification employed below is based on that in Andrews & al. (1967). The taxonomy of the groups represented below is in need of review, and for this reason sources of reference are given for the lower taxonomic categories only.

Abbreviated synonymies are given throughout this paper. For further information, see Woodward (1891).

> Class Selachii Order Hybodontiformes Maisey, 1975 Family Hybodontidae Owen, 1846 Genus ACRODUS Agassiz, 1839 Acrodus minimus Agassiz, 1839 (Pl. 1, Figs 1---3)

Acrodus minimus Agassiz; Agassiz, 3, p. 145, Pl. 22, Figs 5-12. 1839. 1839. Acrodus acutus Agassiz; Agassiz, 3, p. 146, Pl. 22, Figs 13-15, Thectodus inflatus Meyer & Plieninger; Meyer & Plieninger, p. 116, Pl. 10, Fig. 20. 1844. Thectodus glaber Meyer & Plieninger; Meyer & Plieninger, p. 116, Pl. 10, Fig. 21, 1844. 1844. Thectodus tricuspidatus Meyer & Plieninger; Meyer & Plieninger, p. 116, Pl. 10, Fig. 27; Pl. 12, Fig. 29.

Material: 23 teeth, mostly fragmentary.

Description. — The complete teeth studied vary from 2 mm to 4 mm in length, the average being 3 mm long. The specimens comprise tooth crowns only in all cases, the roots having been detached. The crown is elongate and bears a median principal cusp, which is either low, or of medium height. The height of the crown measured at the principal cusp (from cusp apex to crown base) varies from 0.7 mm to 1.3 mm. The shoulder of the crown is at its thickest toward the base of the median cusp, and the width of the tooth at this point varies between 0.7 mm and 1.3 mm. Very low lateral cusps may be developed on either side of the median cusp, but these are not obvious in the specimens studied. A long ridge or keel (crista longitudinalis) passes from end to end of the crown, intersecting the median and lateral cusps at their apices. The sides of the crown fall away from this ridge to the crown shoulder. A tubercle is occasionally developed at the base of the median cusp on the labial side, and may become quite prominent. A longitudinal ridge connects the tubercle, when it is present, with the apex of the principal cusp, giving a diamond-shaped outline to the base of the cusp in apical view. Other longitudinal, fine to coarse striations arise from the cusp apices and the *crista longitudinalis*, and pass down toward the base of the crown, terminating at the crown shoulder. The crown is undercut on the lingual side by a face sloping toward the crown/root junction. On the labial side, this junction is located just under the crown shoulder. The underside of the crown is concave for the reception of the root.

The teeth of this form vary slightly in outline according to their position in the mouth, and possibly also according to their stage in ontogeny. Some teeth are quite strongly arcuate with broad, flat crowns (Pl. 1, Fig. 1) while others are narrow and elongate (Pl. 1, Figs 2-3). The remainder are intermediate between these two extremes.

Occurrence. - Lejowa Valley.

Genus HYBODUS Agassiz, 1837 Hybodus cf. cloacinus Quenstedt (1858)

Description. — One collected fragment is obviously the base of a cusp and the crown of an hybodont tooth. Fairly coarse longitudinal striations ascend the crown, suggesting some affinity with the teeth of Hybodus cloacinus. The tooth fragment is too incomplete to allow any confident conclusions as to its specific affinities.

Occurrence. - Lejowa Valley.

Indeterminate selachian dermal denticles

The dermal denticles obtained from the samples can be divided into members of two morphological types. The nomenclature employed by Applegate (1967) will be used, in which the denticle is divisible into basal plate, pedicel and crown (Text-fig. 2).

PEDICEL Fig. 2 Nomenclature of dermal denticle BASAL PLATE · · morphology

Type 1 Dermal Denticles (Text-fig. 3a—b)

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Description. — Denticles (6 specimens) of this morphological type are commonly known as "placoid scales". Previously figured and described as "Nurretla" sp. by Gaździcki (1974; Pl. 51, Figs 11—13), these denticles measure up to 1 mm from the base to the crown apex. The basal plate is expanded to give good anchorage in the dermal tissues. The undersurface is flat to minimally concave, and the overall shape of the basal plate is sub-circular to sub-quadrate

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in the specimens studied. The upper surface of the basal plate is ornamented by a series of coarse striations which extend up the fairly robust pedicel, but terminate at the base of the crown in most cases.

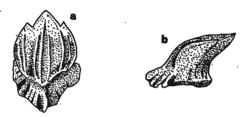


Fig. 3. Dermal denticle, Type 1: a oblique anterior view (cf. Gaździcki 1974; Pl. 51, Fig. 13), b side view; \times 42

The pedicel is quadrate in cross section. The crown is angled away from the pedicel to project posteriorly (Text-fig. 3b, see also Gaździcki 1974, Pl. 51, Fig. 13). The crown is generally lanceolate in outline, and terminates in a point. Several lateral apices may also be developed. Longitudinal keels may develop on the anterior face of the crown (Text-fig. 3b). These keels are usually concentrated in median and flanking areas. The keels themselves arise from the top of the pedicel, at the shoulder of the anterior face of the crown. The median set of keels bifurcate from a prominent ridge on the pedicel, which continues as a prominent ridge on the basal plate. Similarly, the lateral keels develop from other prominent ridges on the pedicel and basal plate. These prominent ridges define the corners of the basal plate in cases where it is quadrate. The keels fail to reach the crown apices. The posterior face of the crown has no ornament.

Occurrence. — Mt. Hradok and Lejowa Valley,

Type 2 Dermal Denticles (Pl. 1, Figs 5-6 and Text-fig. 4a-b)

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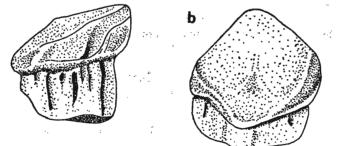


Fig. 4. Dermal denticle, Type 2: a side view, b oblique anterior view; \times 35

Description. — The denticles (9 specimens) in this group measure up to 1 mm high, and 1 mm across. They differ from the denticles of Type 1 in that the basal plate is indistinguishable from the very well developed, high, robust pedicel. The shape of the basal plate is oval to quadrate, with a small foramen

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developed in the centre of the undersurface. No such foramen appears to be present in the denticles of Type 1. Coarse longitudinal striae are present on the pedicel, terminating at the pedicel/crown junction. The crown is usually quite smooth, occasionally showing evidence of ante-mortem wear. In some cases, there is a suggestion of keel development on the crown. In all the specimens, the crown is far more robust than the condition found in members of Type 1. Also, the crown projects posteriorly in only a few cases, usually being roughly circular in shape. In specimens with the latter crown shape, keels are developed on the crown shoulders, but not on the upper surface.

Occurrence. - Lejowa Valley.

Class Actinopterygii Subclass Chondrostei Order Palaeonisciformes Family Birgeriidae Aldinger, 1937 Genus BIRGERIA Stensiö, 1919 Birgeria acuminata (Agassiz, 1839) (Pl. 1, Fig. 8)

1839. Saurichthys acuminatus Agassiz; Agassiz, 2, pp. 86-87, Pl. 55a, Figs 1-6.
1921. Birgeria acuminatus (Agassiz); Stensiö, pt. 1, p. 150.
1966. Birgeria acuminata (Agassiz); Savage & Large, Palaeontology 9, pp. 135-141.
Material: 13 complete and fragmentary specimens.

Description. — The teeth are conical in shape, measuring up to 2 mm high, and 0.9 mm across the base. The tooth is upright, occasionaly with slight posterior curvature, and possesses a translucent enamel apical cap which extends to a point just over half way down the shaft of the tooth in complete specimens. This apical cap may be slightly flattened, with the rest of the tooth, and possess two cutting edges. The apical cap is separated from the base of the tooth by a collar. From this collar arise a series of longitudinal striations, which extend up the apical cap toward the tooth apex, but never actually reach it. The lower part of the tooth is also ornamented by a series of longitudinal striations, although these are much finer and more closely spaced than those on the apical cap. The pulp cavity is moderately developed at the base of the tooth, forming about one third of the total base diameter. The pulp cavity extends very high up the shaft of the tooth, terminating just before the tooth apex.

Occurrence. - Lejowa Valley and Mt. Hradok.

Suborder Palaeoniscoidei Family Palaeoniscidae Vogt, 1852 Genus GYROLEPIS Agassiz, 1835 Gyrolepis albertii Agassiz, 1835 (Text-fig. 5 and Pl. 2, Fig. 1)

1835. Gyrolepis albertii Agassiz; Agassiz, 2, p. 173, Pl. 19, Figs 1-6.
1835. Gyrolepis tenuistriatus Agassiz; Agassiz, 2, p. 174, Pl. 19, Figs 10-11.
1835. Gyrolepis maximus Agassiz; Agassiz, 2, p. 175, Pl. 19, Figs 7-9.
Material: 4 teeth, 18 scale fragments.

Description of the teeth. — The teeth are conical, upright, but slightly smaller than those of *Birgeria acuminata* and *Saurichthys longidens*, measuring up to 1.2 mm high, and 0.5 mm across the tooth base. The apical cap is restricted

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to the upper third of the tooth, and is unornamented. The shaft of the tooth appears to be very finely striated in one of the specimens studied. The pulp cavity is small, comprising a maximum of only one third of the tooth base diameter. The nature of the specimens studied does not allow consideration of the degree of penetration of the pulp cavity up the shaft of the tooth.



Fig. 5

Tooth of Gyrolepis albertii Agassiz; side view, \times 35

Description of the scales. — The scales studied are all fragmentary, many showing evidence of post-mortem wear. The largest is almost complete, rhomboidal in shape, and measures 2 mm long by 2 mm deep (Pl. 2, Fig. 1). The distinguishing feature on all of these scale fragments is the existence of an area of enameloid ganoin. This exposed portion of the scale is several layers thick. The ganoin is ornamented by a series of diagonal ridges which may bifurcate in places, but which are truncated by the boundary of the rhomb exposed in life. The bony base of the scale measures up to 0.7 mm thick, and is itself rhomboidal in shape. The base of the anchoring projections are discernible in one specimen. The back, or internal face of the scale is usually flat, but may thicken toward the centre.

Occurrence. — Lejowa Valley.

Order Saurichthyiformes Family Saurichthyidae Goodrich, 1909 Genus SAURICHTHYS Agassiz, 1834 Saurichthys longidens Agassiz, 1834 (Pl. 1, Fig. 7)

1834. Saurichthys longidens Agassiz; Agassiz, 2, p. 87, Pl. 55a, Figs 17—18 Material: 9 teeth, virtually complete.

Description. — These teeth are also conical, measuring up to 2 mm high, and 1 mm across the base. The teeth are upright, and generally sigmoidal in shape, if curved. The translucent apical cap is restricted to the upper third of the tooth, and lacks striations. The shaft of the tooth is long, and is expanded at the base. Coarse striations run the length of the shaft to terminate at the base of the apical cap. The pulp cavity is very wide at the base, forming as much as $80^{\circ}/_{\circ}$ of the base diameter, but is constricted to a smaller channel near the shaft base. In the specimens studied, the pulp cavity terminates some distance below the apical cap, approximately two thirds of the way up the shaft of the tooth.

Occurrence. - Lejowa Valley and Mt. Hradok.

Order **Perleidiformes** Family **Colobodontidae** Stensiö, 1916 Genus COLOBODUS Agassiz, 1844 Colobodus sp. (Pl. 2, Fig. 2)

Material: 5 teeth, 1 scale fragment.

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Description of the teeth. — The teeth are small, measuring a maximum of 0.8 mm across the crown, and are dome-shaped. The teeth characteristically possesses a small apical tubercle, about one third of the total crown diameter in width (cf. Pl. 2, Fig. 2). This tubercle is a small area of "modified dentine" (Guttormsen 1937, Peyer 1968) sitting in a larger area of true enamel. In some specimens, striations are developed in the true enamel, and radiate from the central tubercle. The root is not preserved in any of the specimens studied, but the underside of the crown shows that the root wall varies from being thin, to relatively thick, the pulp cavity comprising up to three quarters of the root diameter.

Description of the scale. — The single scale fragment tentatively identified as belonging to Colobodus, consists of a small portion of the ganoin rhomb. It is distinguished from the scales of Gyrolepis in that the diagonal ridges on the exposed rhombic ganoin area are much coarser, and tend to be well separated from each other.

Occurrence. - Lejowa Valley.

Subclass Holostei Division Holosteans Order Seminotiformes Family Semionotidae Genus SARGODON Plieninger, 1847 Sargodon tomicus Plieninger, 1847 (Text-figs 6-7)

1847. Sargodon tomicus Plieninger; Plieninger, p. 165, Pl. 1, Figs 5—10. Material: 1 incisiform and 3 molariform teeth.



Fig. 6 Molariform tooth of Sargodon tomicus Plieninger; side view, \times 18

Description. — The teeth of this form are divisible into two morphological types. There is an incisiform type, and dome-like crushing tooth type. One specimen of the former was found in the sample, and proved to be the largest single vertebrate fragment, measuring 3.5 mm high, 4.8 mm long, and 2 mm wide. The root is missing. The crown is upright, and oblong in basal cross section. The lingual and labial faces converge into a long cutting edge forming the crown apex. The labial face is convex, the lingual face concave. Ante-mortem wear on the tooth has produced a V-shaped notch in the cutting edge of the crown.

The three dome-shaped teeth are circular in basal cross section, again, only their crowns being preserved. The crown is featureless, lacking the pad of dentine and striations found in *Colobodus*. The largest of the three specimens measures 1.4 mm across the base, and 1 mm high. The undersurface of the crown

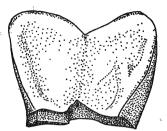


Fig. 7 Incisiform tooth of Sargodon tomicus Plieninger; lingual view, \times 8

is markedly concave, and the root walls thin. Tooth histology is characteristic for this species, having been described by Guttormsen (1937) and others. Worn teeth of both morphological types often show large dentine tubules exposed, or lying just beneath the crown surface.

Occurrence. — Lejowa Valley.

Family Lepidotidae Owen, 1860 Genus PARALEPIDOTUS Stolley, 1920 ?Paralepidotus sp.

Description. — The only collected tooth is broken in half, and measures only 0.7 mm across the base. There is a small central tubercle on the dome-shaped crown. The crown is formed entirely of true dentine, and lacks the pad of dentinal tissue seen in Colobodus. Also, there appears to be no presence of bundles of dentine tubules, such as are found in Sargodon. The shape of the dentine mass appears to most closely resemble the condition found in Paralepidotus, as described by Guttormsen (1937). The root is missing, but the undersurface of the crown is markedly concave, and indicative of a wide pulp cavity. The teeth of Paralepidotus figured by Guttormsen appear to have a rather narrower pulp cavity than the specimen described here. Thus the tooth is only tentatively assigned to the genus Paralepidotus.

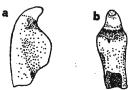
Occurrence. — Lejowa Valley.

Indeterminate Actinopterygian remains

Tooth Type 1 (Text-fig. 8a-b, and Pl. 1, Fig. 4)

Description. — The only collected tooth is hook-shaped, and measures 0.7 mm high, and 0.5 mm across the widest part (see Text-fig. 8a—b). The tooth has a wide pulp cavity, and is more slender at the base, widening toward the shoulder. The robust apical cap is translucent and somewhat recurved. The

Fig. 8 Gill raker tooth of ?Sargodon tomicus Plieninger: a side view, b front view; \times 42



specimen could well be a gill raker tooth, and as such may have derived from Sargodon tomicus Plieninger.

Occurrence. — Lejowa Valley.

Tooth Type 2 (Pl. 1, Figs 10-11)

Description. — The three collected teeth are quite large (1.8 mm high, 0.5 mm across the base) and upright, although slightly recurved. There is no distinct apical cap. The pulp cavity is wide, and the base of the tooth is slightly narrower than the tooth shoulder. Again, the teeth may come from Colobodus or Sargodon, or from an as yet unknown actinopterygian.

Scales (Text-fig. 9a-b and Pl. 1, Fig. 12a-b)

Description. — The scales (10 specimens collected) all show a reduced thickness of ganoin on the external face, indicative of an advance beyond the palaeoniscid grade of evolution in the actinopterygians. Some of the more fragmentary remains lack a ganoin covering completely, but in at least some cases this may be due to post-mortem wear. Thus, certain specimens may represent highly eroded palaeoniscid scales, and as such, may in fact pertain to Gyrolepis.

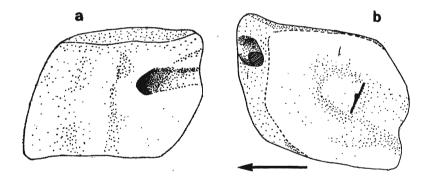


Fig. 9. Lateral line scale of ?Sargodon tomicus Plieninger: a internal view, b external view (arrow directed anteriorly); \times 20

One excellently preserved specimen (Text-fig. 9a—b and Pl. 1, Fig. 12a—b), is a scale with greatly reduced ganoin coat, measuring 2.5 mm long, and 2 mm deep. The scale is from a position on the lateral line of the parent fish. The lateral line canal enters the scale at a point high up on the anterolateral border on the external face, and exits just posterior to the midline on the internal face. A subsidiary canal branches off from this main lateral line canal near the centre of the scale, and opens on the exterior face. The foramen is protected by an overhanging development of the ganoin and is located near the centre of the external face. The most likely candidate for this scale to have come from is *Sargodon tomicus*, since this is the only holostean present in the fauna.

In addition to those described above, there is a single example of a scale fragment with a peculiar stippled ornament on the external face.

Occurrence. — Lejowa Valley.

? Fin rays (Pl. 1, Fig. 9)

Description. — The six collected specimens are small (less than 1 mm high), narrow, slightly curved structures, lacking pulp cavity, and, in the case of terminal fragments, possessing a small apical cap.

Vertebrae (Text-fig. 10a-b)

Material. — 2 specimens.

Description. — One specimen is a small (less than 1 mm) ring centrum. The other is larger (3 mm across, 2 mm deep), and is a barrel-shaped biconcave centrum preserving a very narrow notochordal canal, with no other distinguishing features.

Occurrence. - Lejowa Valley.

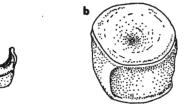


Fig. 10. Vertebrae: a ring centrum in end view, \times 18; b centrum in oblique view, \times 10

Other phosphatic remains

In addition to the vertebrate remains described above, the bone-bed sample from Lejowa Valley yielded phosphatised invertebrate remains. These include a single internal cast of a gastropod, some internal casts of small pelecypods, and four examples of invertebrate coprolites.

DISCUSSION

TAPHONOMY

Bone beds are common lithological types in the European Rhaetic (cf. Barth 1968; Sykes 1971, 1974, 1977). The best known areas of their occurrence are in the relatively shallow water sequences of the Germano-British Basin. The British examples are primarily of secondary origin, comprising prefossilised vertebrate remains.

The concept of prefossilisation was first dealt with in depth, and with reference to bone bed deposition, by Reif (1971). Reif considers that during diagenesis, the density of the skeletal fragments is increased, often to a level close to that of quartz sand, and collagen is broken down, thereby reducing the inherent elasticity of the bone. As fossilised bones are reworked from source areas, transported and redeposited, the now brittle vertebrate fragments are extremely susceptible to fracture and polishing. Thus, the particular features of prefossilised vertebrate remains are high polish, distinctive fracture pattern, and deposition with clastic material of similar density (equivalence principal). Deposits containing prefossilised vertebrate remains may be expected to show considerable diversity in sedimentological maturity, however. The researches of the senior author have shown that, in Britain, three bone bed types can be discerned. Well-sorted bone beds ("secondary") composed almost totally of prefossilised vertebrate remains are common in the Westbury Beds. These bone beds are associated with comparatively high energy depositional conditions. In contrast, horizons containing vertebrate remains which have not been prefossilised — primary bone beds — have been located in the Westbury Beds at such localities as Blue Anchor Point, Somerset. A bone bed type containing both prefossilised and primary vertebrate remains — the intermediate bone bed type — is exemplified by the basal, conglomeratic bone bed overlying the Tea Green Marl at Aust Cliff, Avon, and also represented by a bone bed in the middle of the Westbury Beds as exposed at Westbury Garden Cliff, Gloucestershire. Parallel, but independent work has been conducted by Mr. J. H. Sykes (*in press*), who has reached similar conclusions by using a slightly different approach.

In Germany, the work of Reif has been amplified by Aepler (1974) with reference to the Rhaetic deposits of the Tübingen area. Potential primary bone beds were deposited in the lagoonal sediments between channels on a prograding Rhaetic delta. With conditions of reasonably stable sea level, the transported sediment choked the river channels, causing switching. This channel switching reworked the previously deposited vertebrate remains, concentrating them as secondary, lag conglomerate bone beds. The transgression of the Early Liassic sea over the delta sandstones reworked both bone bed types, depositing a transgressive secondary bone bed, with a good deal of faunal mixing.

Rhaetic bone bed deposits are also found in north Germany, and the condensed Rhaetic sequence of western Switzerland, which latter deposits mark the peleogeographical transition between Tethys and the Germano-British Basin. Rhaetic deposits in France, Luxembourg, and even the platform complexes of the Dachsteinkalk of the northern Alps, preserve bone bed lithologies. Bone bed deposition in the generally deeper water Carpathian and Swabian facies of the Carpathians are much less common.

The vertebrate remains described above from the two stratigraphic sections, are of small size, showing very little or no polish. Wear on the specimens of fish teeth is nearly all ante-mortem. Many of the teeth and scales are broken, but the fracture patterns suggest that breakage occurred during primary deposition, or even during extraction of the material, rather than during post-fossilisational history. The fact that the samples studied represent the residue of some 15 kg of matrix, even though called a bone bed, precludes effective concentration, and extensive transportation of the vertebrates alongside the invertebrates having taken place.

It is most likely, therefore, that the bulk of the vertebrate remains

are primary, and not prefossilised, and that they have been incorporated into sediments laid down in close proximity to the site of death or shedding (*i.e.* minimally allochthonous). This is especially true for the Mt. Hradok material. The hand specimen of the Lejowa Valley bone bed (Pl. 2, Fig. 3) contains vertebrate remains which appear to be prefossilised, even though most of the extracted remains are of primary appearance. Thus, it may be that this bone bed contains a mixture of primary and prefossilised elements. Certainly, the presence of phosphatised invertebrate remains suggest that at least some of the bioclastic material was subject to diagenesis prior to eventual burial and final incorporation into the bone bed lithology.

The fact that the vertebrate remains from both localities are not articulated indicates that bottom currents were sufficient to break up decaying carcasses and redistribute the skeletal elements.

Certain faunal elements, such as the hybodont teeth, may conceivably have been shed by the living animal directly above the site of ultimate burial. The association of vertebrate remains with invertebrates in the sub-tatric Rhaetian bone beds is a feature common to other areas (cf. Barth 1968).

SIGNIFICANCE OF THE FAUNA

The faunas described above, even though numerically small, show a rich and diverse association of fish remains. Despite the fact that the samples were obtained from small-scale bulk breakdown of matrix, the true significance of the faunas is not easily judged. This is primarily due to the paucity of representative, well-documented equivalent faunas from Poland, and other Carpathian and Alpine areas. Certainly, all of the forms named and described above are typical of European Rhaetic deposits (cf. Barth 1968). The record of *Colobodus* is to our knowledge, only the second confident determination of this genus from deposits of Rhaetian age. The other elements of the faunas are all well documented from British and German localities.*

The dermal denticles of Type 1 compare quite closely with those described by Sykes (1974) from the Rhaetic of the East Midlands of England. Both those described above, and those described by Sykes are definitely of euselachiform organisation. Euselachiform remains from the Upper Triassic will be reviewed elsewhere by the senior author.

It is notable that no teeth of Hybodus minor Agassiz, and only one doubtful fragment of a tooth of H. cloacinus Quenstedt were found in the samples. Both of these forms are common in the Rhaetian of most

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^{*} Possible exceptions are the actinopterygian tooth types 1 and 2. Similar teeth have been found by C. J. Duffin from certain other European sites, but are as yet undescribed, and will be discussed in more detail elsewhere.

other European localities, the former more so than the latter. Their absence from the sub-tatric Rhaetian faunas may be due to an artifact of sampling, to some sorting of the vertebrate remains prior to final deposition, or to their complete exclusion as a result of other, as yet indeterminate, paleoecological factors. The true reason may be better discerned with the discovery and quantitative documentation of new faunas.

Larger faunal elements, such as fin spines (cf. *Hybodus, Nema*canthus monilifer) and the remains of aquatic reptiles (placodonts, ichthyosaurs, plesiosaurs and ?*Rysosteus oweni*) tend to be uncommon, in comparison with the quantitative representation of the fish remains, in other bone beds. Their absence from the faunas described above is therefore not necessarily significant.

Crushing teeth of the dipnoan, *Ceratodus*, are reasonably common in the European Triassic in general. It may well be that *Ceratodus* was restricted to fresh or brackish water, and would therefore not be expected to be represented in the sub-tatric Rhaetian faunas. The rich invertebrate faunas found at the sections from which the vertebrate samples came, indicate a thoroughly marine environment of deposition (cf. Gaździcki 1974). It should be noted that Roemer (1870) records *Ceratodus* from the Polish Lower Rhaetian (Lisów and Woźniki areas of the Silesia-Cracow Upland), but this was in association with other remains of distinctly brackish (freshwater) terrestrial influence (reptile bones *Mastodonsaurus* sp., *Termatosaurus* albertii Plieninger, *Megalosaurus* cloacinus Quenstedt, and the ostracode *Darwinula* sp.).

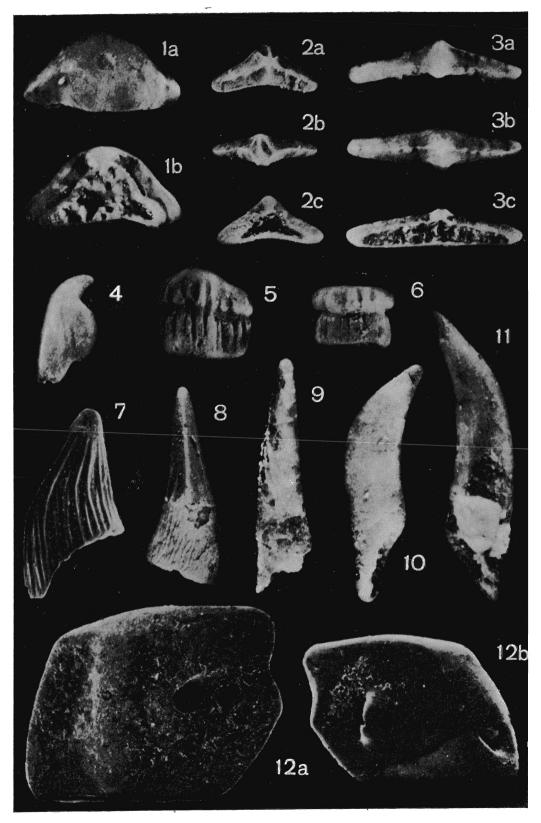
CONCLUSIONS

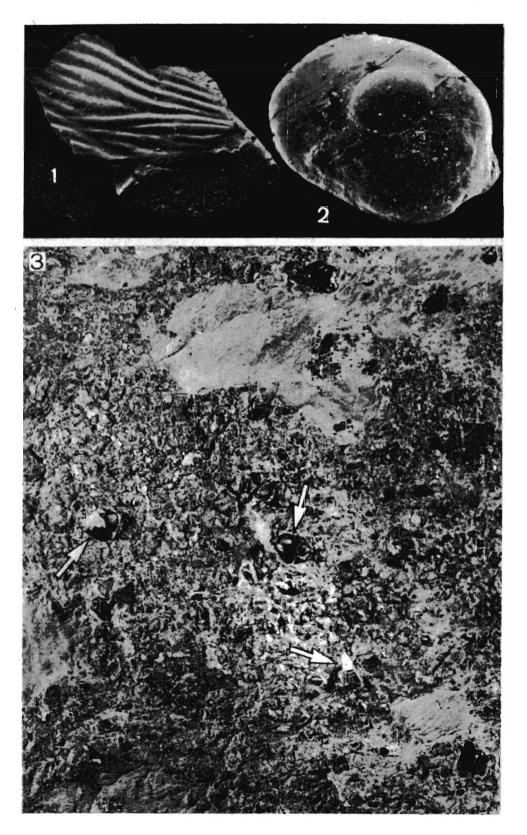
The faunas obtained from the Rhaetian rocks of the Tatra Mountains, although numerically small, contain considerable diversity of species representation. Teeth of the hybodont shark *Acrodus minimus* Agassiz are common, together with teeth of the palaeoniscid chondrosteans *Birgeria acuminata* (Agassiz), *Saurichthys longidens* Agassiz,

PLATE 1

1	Tooth of Acrodus minimus Agassiz: a slightly oblique apical view, b slightly oblique basal view; \times 20
7	
2	Tooth of Acrodus minimus Agassiz: a apical view, b labial view, c basal view;
	× 15
3	Tooth of Acrodus minimus Agassiz: a labial view, b apical view, c basal view;
	\times 15
	4 Gill raker tooth of ?Sargodon tomicus Plieninger; side view, $ imes$ 35
	5—6 Dermal denticles, Type 2; side view, \times 27
	7 Tooth of Saurichthys longidens Agassiz; side view, \times 50
	8 Tooth of Birgeria acuminata (Agassiz); side view, \times 27
	9 ?Fin ray, × 60
	10-11 Actinopterygian teeth, Type 1; side view, \times 37
	12 Holostean scale: a internal view X 22: b external view X 10

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and Gyrolepis albertii Agassiz. The species Sargodon tomicus Plieninger is also well represented. The genus Colobodus is confidently identified in the fauna. Less certain identifications are made of Paralepidotus and Hybodus cloacinus Quenstedt. Other, as yet indeterminate fish remains include a lateral line scale belonging to an holostean (possibly Sargodon tomicus Plieninger), and some euselachiform dermal denticles.

There are few usefully comparable faunas from other Carpathian sites, and localities of similar facies development. Comparison with other European faunas, particularly those of the Germano-British Basin, indicates that the described fish remains represented in the Tatra Rhaetian are all well documented from other sites. The absence of $Hybodus\ minor$ Agassiz and the single report of H. cf. cloacinus Plieninger in the fauna may be due to sorting, or to other paleoecological factors.

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PLATE 2.

Scale of Gyrolepis albertii Agassiz; external view, × 30
 Tooth of Colobodus sp.; oblique apical view, × 100
 Hand specimen (magnified twice) of bone bed from Lejowa Valley; the best preserved vertebrate remains are arrowed

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SZCZĄTKI RYB Z RETYKU REGLOWEGO TATR

(Streszczenie)

W profilach retyku reglowego w rejonie Doliny Lejowej oraz Hradka w Tatrach (fig. 1) znaleziono fragmenty warstwy kostnej (bone bed) zawierającej dobrze zachowany, bogaty i zróżnicowany zespół szczątków ryb (por. fig. 1—10 oraz pl. 1—2). Analizowane szczątki obejmują głównie zęby i łuski, ponadto ząbki skórne oraz nieoznaczalne elementy różnych części szkieletowych. Większość powyższych szczątków należy do form z rzędu Selachii (żarłacze) oraz podgromady Actinopterygii (promieniopłetwe). Żarłacze reprezentowane są głównie przez Acrodus minimus Agassiz, rzadziej Hybodus cf. cloacinus Quenstedt, natomiast wśród promieniopłetwych dominują Birgeria acuminata (Agassiz), Gyrolepis albertii Agassiz, Saurichthys longidens Agassiz, Sargodon tomicus Plieninger oraz Colobodus sp. Badany zespół szczątków ryb nawiązuje wyraźnie do równowiekowych zespołów znanych z Północnych Alp Wapiennych (por. Barth 1968), a także wykazuje pewne analogie do zespołów z warstw kostnych epikontynentalnych osadów retyku północno-zachodniej Europy (por. Schmidt 1928; Sykes 1971, 1974, 1977).