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Vertebrate remains from the Lower Muschelkalk of Raciborowice Górne (North-Sudetic Basin, SW Poland)

Alina CHRZĄSTEK

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Vertebrate remains, mostly fish teeth and scales, are described from the Lower Muschelkalk of Raciborowice Górne, North-Sudetic Basin, SW Poland. The assemblage occurs in dark grey organodetrital limestone of unit C. Vertebrate remains, represented mainly by vertebrate bones and coprolites, are also known from unit B. Five taxa of chondrichthyan teeth — *Acrodus lateralis*, *Acrodus* cf. *lateralis*, *Acrodus* sp., *Palaeobates angustissimus*, *Palaeobates* sp. and, for the first time from this region, two taxa of osteichthyan remains — teeth of *Birgeria* sp., scales from *Gyrolepis* sp. as well as scales from unclassified actinopterygians and enigmatic bones (fishes?) are described from the Lower Muschelkalk at Raciborowice Górne. Reptile teeth representing the Nothosauridae or Cymatosauridae have been found for the first time at this locality. They were discovered in the Bone Bed of unit C, that had previously only yielded fish teeth. The material collected has allowed reconstruction of the vertebrate assemblage of the Lower Muschelkalk of the North-Sudetic Basin. It has also helped to constrain reconstructions of the palaeoenvironment, suggesting that it represented a deepening lagoon. The assemblage has been correlated with age-equivalents from other regions of Europe, the faunas from the Holy Cross Mts. (Central Poland) being the closest analogy. The evidence indicates that, during the deposition of units B and C that, contain the vertebrate remains, connection with the Tethys Ocean was through the Silesian–Moravian and East Carpathian marine gateways.

Alina Chrząstek, Institute of the Earth Sciences, Wrocław University, Maksa Borna 9, PL-50-204 Wrocław, Poland; e-mail: alina.chrzastek@ing.uni.wroc.pl *(received: February 18, 2008; accepted: June 16, 2008).*

Key words: North-Sudetic Basin, Lower Muschelkalk, vertebrate remains, fish teeth, Chondrichthyes, Osteichthyes.

INTRODUCTION

The first record of vertebrate remains from the North-Sudetic Basin (Noetling, 1880) mentioned teeth and bones of fish and labyrinthodont amphibians from the Roetian near Raciborowice Górne as well as fish scales and reptile teeth from the Lower Muschelkalk near Stara Warta. The fossils comprise *Colobodus chorzowiensis* Mey, *Gyrolepis* sp., *Pleurolepis silesiacus* Eck., *Placodus* sp. and *Nothosaurus* sp. Holdefleis (1915) reported the occurrence of fish scales and vertebrate bones in the Lower Muschelkalk at Raciborowice Górne.

Chrząstek (1995*a*, *b*) discovered a tooth of the selachian *Lissodus* sp. in the Roetian near Czapla and reported beds of unit A of the Lower Muschelkalk at Jerzmanice Zdrój abounding in fish scales. She also characterized an assemblage consisting of skeletal remains of fishes, amphibians and reptiles from units B and C exposed at Raciborowice Górne (Chrząstek, 2002). It comprised *Acrodus lateralis*, *Acrodus* cf. *lateralis*, *Acrodus* sp., *Palaeobates angustissimus*, *Palaeobates* sp., *Nothosaurus* cf. *mirabilis* and *Nothosaurus* sp. Vertebrate remains from the Roetian and Lower Muschelkalk of the North-Sudetic Basin and Opole region were also described by Chrząstek and Niedźwiedzki (1998).

Recent investigations have resulted in the discovery of an assemblage of chondrichthyan teeth: *Acrodus lateralis*, *Acrodus* cf. *lateralis*, *Acrodus* sp., *Palaeobates angustissimus* and *Palaeobates* sp. Osteichthyan teeth and scales (*Gyrolepis* sp., *Birgeria* sp. and other actinopterygians) as well as reptile teeth (Nothosauroidea or Cymatosauroidea) and bones of unknown taxonomy have been reported from the Lower Muschelkalk at Raciborowice Górne for the first time.

GEOLOGICAL SETTING

The best and most complete section of the Lower Muschelkalk in the North-Sudetic Basin crops out in the Grodziec Syncline at Raciborowice Górne and its fragments are exposed in the Leszczyna Syncline at Jerzmanice Zdrój

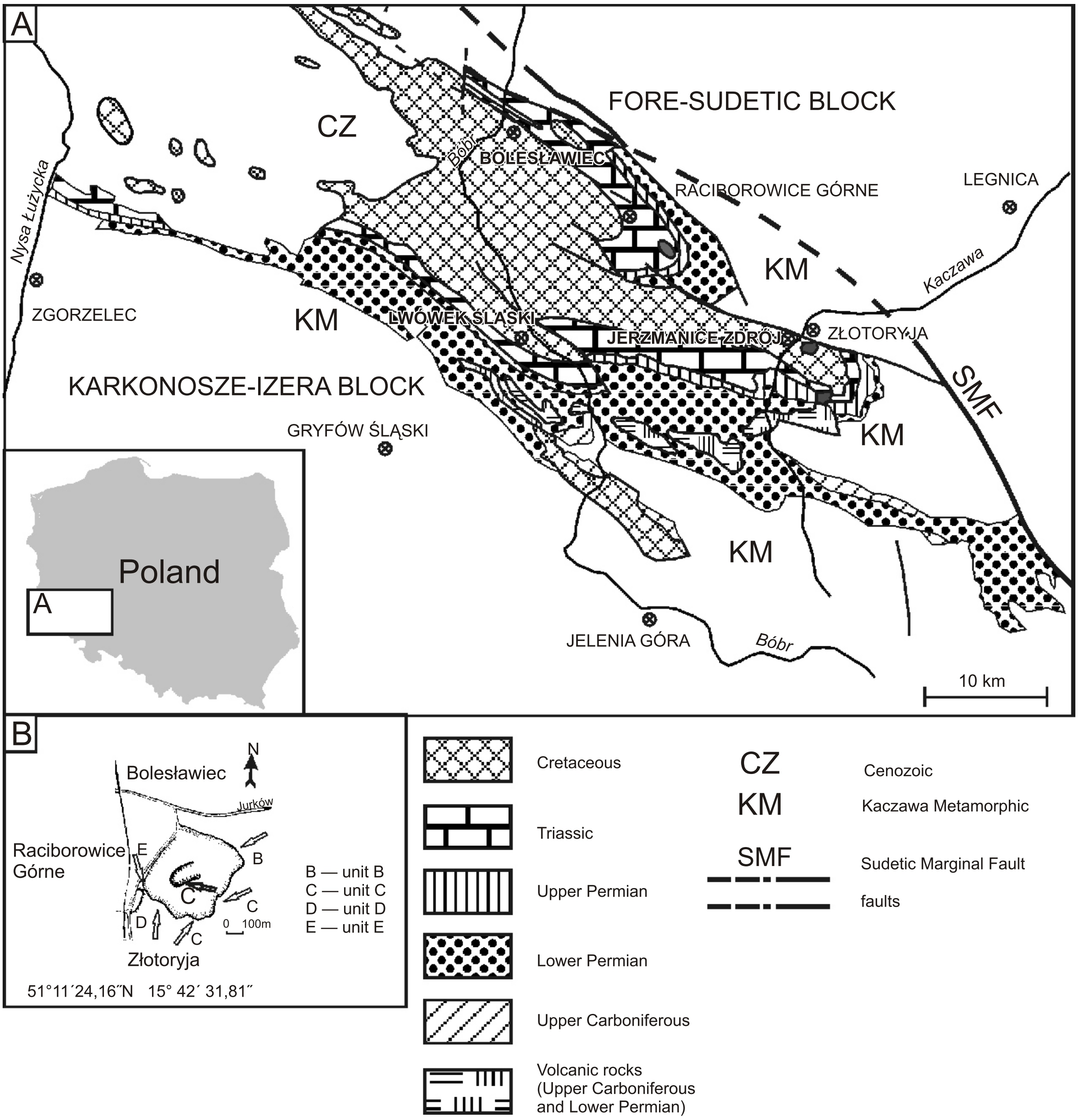

Fig. 1A — geological map of the North-Sudetic Basin after Sawicki and Teisseyre (1978), modified by the author; B — schematic plan of the Raciborowice Górne quarry with places where individual units (B–E) are exposed are marked

(Chrząstek, 1995*b*, 2002; Fig. 1). In the North-Sudetic Basin, apart from the Triassic rocks, sequences of Upper Carboniferous, Permian, Lower Cretaceous and Cenozoic strata crop out, overlaying the Eocambrian–Lower Carboniferous basement (Baranowski *et al.*, 1990). A detailed analysis and lithostratigraphic subdivision of the Lower Muschelkalk into units A–E were given by Chrząstek (2002). The same deposits were also described by Leśniak (1978) and Szulc (1991).

Unit A is exposed only at Jerzmanice Zdrój. In the Raciborowice Górne quarry the Lower Muschelkalk section commences with unit B, represented by thick-bedded crinoid-rich organodetrital limestone in the lowermost part (Głuchowski and Salamon, 2005; Figs. 1 and 2). The remaining part of unit B is built of cellular and thick-bedded organodetrital limestones with occasional intraclasts. Intercalations of thin-bedded platy limestone and marls are common. The deposits of unit B are about 15 m thick.

The strata of unit C are composed of thick-bedded organodetrital limestone with occasional intraclasts, intercalated with thin-bedded wavy or nodular limestones and marls (Figs. 1 and 3). They comprise the *Spiriferina* Bed, a very characteristic correlation horizon that may be traced in the upper and lower levels of the quarry (Holdefleis, 1915; Chrząstek, 2002). The thickness of unit C reaches about 50 m. The upperlying 18 m-thick sequence of thick-bedded oncolitic, crystalline and organodetrital limestones intercalated with wavy, nodular and platy varieties forms unit D. The uppermost part of the Lower Muschelkalk exposed in the North-Sudetic

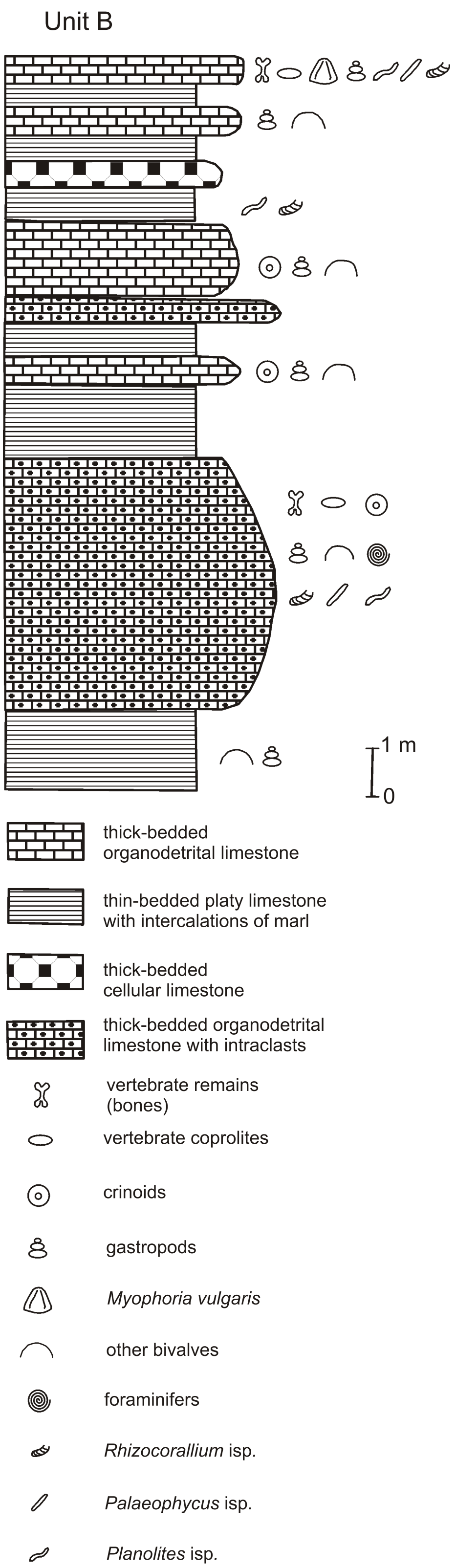

Fig. 2. Lithostratigraphic section of unit B

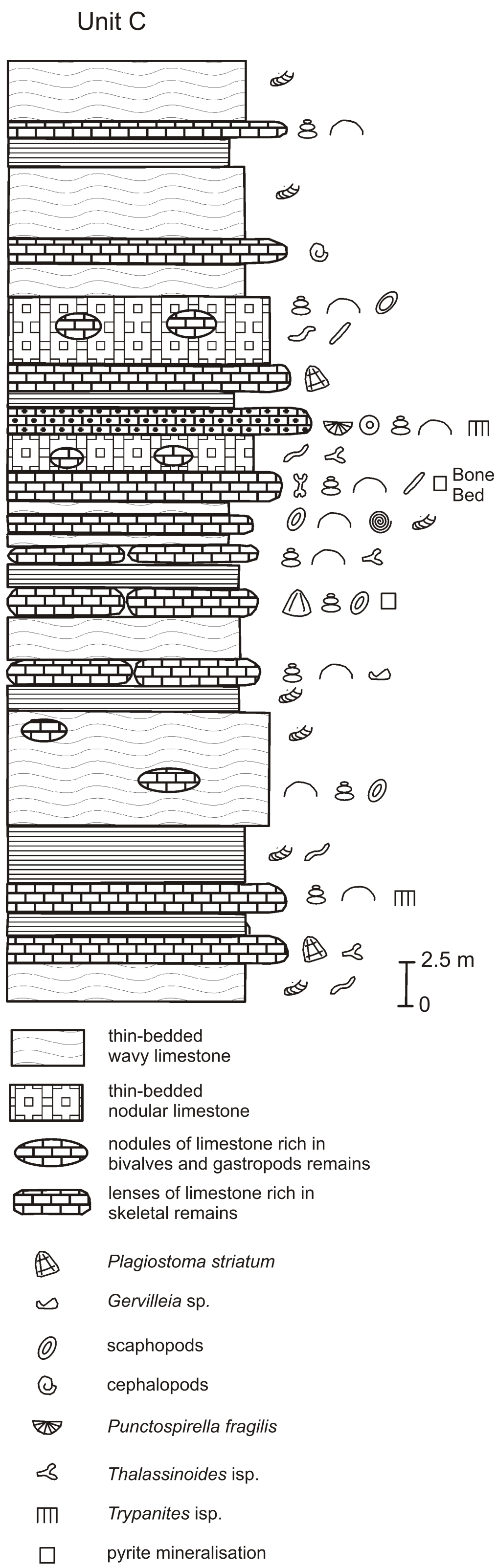

Fig. 3. Lithostratigraphic section of unit C

Other explanations as in Figure 2

Basin is built of the 3.5 m-thick unit E and is represented by fossiliferous (brachiopods and crinoids) thick-bedded organodetrital limestones intercalated with platy and nodular limestones.

VERTEBRATE REMAINS IN THE LOWER MUSCHELKALK

Vertebrate remains are most abundant in units B and C. Bones and coprolites dominate the assemblage in unit B. Poor preservation hinders their precise taxonomic identification though a single vertebra doubtlessly belongs to the reptile *Nothosaurus* cf. *mirabilis*, a taxon known from this locality and described by Chrząstek and Niedźwiedzki (1998) and Chrząstek (2002). Bone remains occur within the thick-bedded organodetrital limestone at the bottom of unit B. The rock abounds also in crinoids of the genus *Dadocrinus* and the species *Holocrinus acutangulus* as well as in bivalves, gastropods and foraminifera (Hagdorn and Głuchowski, 1993; Chrząstek, 2002; Fig. 2). Numerous vertebrate fossils were encountered also in the uppermost part of unit B. They occur within the thick-bedded organodetrital limestone that is rich in the bivalve *Myophoria vulgaris* (Fig. 2). Coprolites are present in all the above-mentioned strata (Fig. 2).

Fish teeth were discovered only in unit C. They occur within a single layer of pyrite-mineralized dark grey organodetrital limestone with abundant gastropods, bivalves and less numerous ichnofossils *Planolites* sp. (Chrząstek, 2007). The layer lies about 4.5 m below the *Spiriferina* Bed, and is composed of thick-bedded organodetrital limestone with hardground intraclasts and the trace fossil *Trypanites* sp. The brachiopod *Punctospirella fragilis* appears in the *Spiriferina* Bed for the first and only time in the entire section of the Lower Muschelkalk. It is accompanied by abundant encrinids, *Holocrinus acutangulus,* bivalves, gastropods and echinoid spines (Chrząstek, 2002; Salamon *et al*., 2003). Głuchowski and Salamon (2005) also described the crinoid *Eckicrinus radiatus*.

Table 1

Taxonomic distribution of the Lower Muschelkalk vertebrate remains from the Raciborowice Górne section

No.	Taxa	Unit B	Unit C
1	*Acrodus lateralis*	–	+
2	*Acrodus* cf. *lateralis*	–	+
3	*Acrodus* sp.	–	+
4	*Palaeobates angustissimus*	–	+
5	*Palaeobates* sp.	–	+
6	*Birgeria* sp.	–	+
7	*Gyrolepis* sp.	–	+
8	*Nothosaurus* cf. *mirabilis*	+	–
9	Nothosauroidea or Cymatosauroidea	+	–

This organodetrital limestone layer contains chondrichthyans: *Acrodus lateralis*, *Acrodus* cf. *lateralis*, *Acrodus* sp., *Palaeobates angustissimus* and *Palaeobates* sp., teeth and scales of osteichthyans: *Birgeria* sp., *Gyrolepis* sp. and other actinopterygians, as well as bones of unknown affinity (Table 1). Reptile bones and teeth (nothosaurids or cymatosaurids) were also noted. The limestone is so rich in vertebrate remains that it may be referred to as a Bone Bed. Bone fossils are not encountered in unit C outside of this layer. I earlier identified a few bone fragments in unit D in Raciborowice Górne (Chrząstek, 2002) and fish scales in unit A in Jerzmanice Zdrój (Chrząstek, 1995*b*).

SYSTEMATIC PALAEONTOLOGY

Taxonomy of chondrichthyans, osteichthyans (actinopterygians) and reptiles after Cappetta (1987), Nelson (1994 in Bürgin, 1999) and Rieppel (2000), respectively. All the specimens described are deposited in the collection of the Geological Museum, University of Wrocław.

Superclass: Pisces
Class: Chondrichthyes Huxley, 1880
Subclass: Elasmobranchii Bonaparte, 1838
Order: Euselachii Hay, 1902
Superfamily: Hybodontoidea Zangerl, 1981
Acrodontidae Casier, 1959
Acrodus Agassiz, 1837
Acrodus lateralis Agassiz, 1837
(Fig. 4A–B)
MGUWr 5387s; 5388s

1928 *Acrodus lateralis*, Schmidt, figs. 927, 928.
1973 *Acrodus lateralis*, Liszkowski, ryc. 2, fig. 10.
1981 *Acrodus lateralis*, Rieppel, fig.11/3.
2001 *Acrodus lateralis*, Dorka, fig. 1/a.
2002 *Acrodus lateralis*, Chrząstek, pl. 23, fig. 1.

M a t e r i a l. — Two well-preserved crowns; the roots are not visible on the rock surface.

D e s c r i p t i o n. — The crowns are oval and elongated. They measure 2.5 and 4 mm in length, 1.5–2 mm in width and 1–1.5 mm in height. The length/width ratio ranges from 1.6 to 2. Crowns are globular centrally, lower and narrow marginally. The crown ornamentation is generally restricted to the central part. It consists of irregular furrows and delicate ridges diverging from the longitudinal crest towards the crowns' edges. The crown profile, ornamentation and size suggest that the teeth belong to *Acrodus lateralis*. They are slightly smaller then the ones described by Rieppel (1981) and Dorka (2001).

O c c u r r e n c e. — Bone Bed of unit C at Raciborowice. The teeth of this species are known from the *Pecten* and *Dadocrinus* horizon of the Gogolin Beds in the Opole region (Chrząstek and Niedźwiedzki, 1998). Liszkowski (1981, 1993) described similar teeth from the Lower Muschelkalk of the Opole region (*Myophoria* Beds, Gogolin Beds, Górażdże Beds and Terebratula Beds) as well as from the Middle and Upper

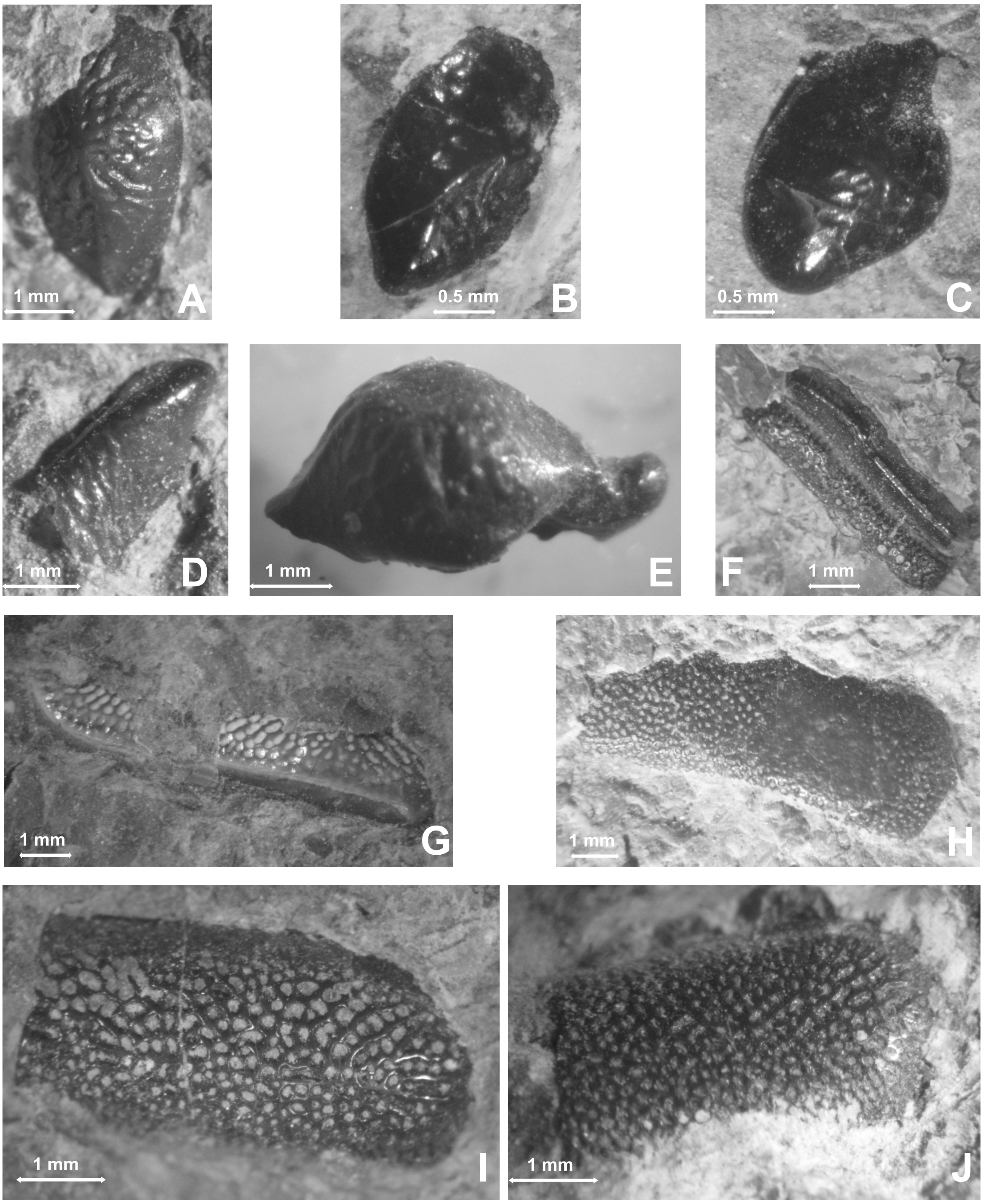

Fig. 4. Fish teeth from the Bone Bed (unit C) of the Lower Muschelkalk at Raciborowice Górne

A–**B** — *Acrodus lateralis*; **C** — *Acrodus* cf. *lateralis*; **D**–**E** — *Acrodus* sp.; **F**–**I** — *Palaeobates angustissimus;* **J** — *Palaeobates* sp.

Muschelkalk. They are most abundant in the Gogolin Beds, Wilkowice Beds and Boruszowice Beds. The author reported the same species from the entire Muschelkalk section except for the middle and upper Middle Muschelkalk of the Holy Cross Mts. It is most numerous within the Ceratite Beds and Łukowa Beds. Schmidt (1928) noted the occurrence of *Acrodus lateralis* in the Lower Muschelkalk and Keuper of Thuringia. Dorka (2001) gave records of *Acrodus lateralis* teeth from the Middle Triassic of Schöningen (Lower Saxony, Germany) while Rieppel (1981) reported it from the Middle Triassic of Monte San Giorgio (Southern Alps, Switzerland).

Acrodus cf. *lateralis*
(Fig. 4C)
MGUWr 5389s

M a t e r i a l. — One well-preserved specimen with poorly marked ornamentation.

D e s c r i p t i o n. — The tooth is oval and rather high. It measures 3–3.5 mm in length, 2–2.5 in width and 2 mm in height. The length/width ratio is 1.4. Faint ornamentation consists of folds running from the crown top toward its margins. The profile and size suggest its assignment to *Acrodus lateralis* but because of the poorly preserved ornamentation it is described as *Acrodus* cf. *lateralis*.

O c c u r r e n c e. — Bone Bed of unit C at Raciborowice.

Acrodus sp.
(Fig. 4D–E)
MGUWr 5390s; 5391s

M a t e r i a l. — Two well-preserved specimens comprise one complete and one fragmentary crown with very weak ornamentation. The latter has one half of the crown missing.

D e s c r i p t i o n. — Teeth are elongated, flat and not very high. The well-preserved ornamentation consists of folds, in places bifurcating, running down from the longitudinal crest. The specimens are 2.5–5 mm long, 1–2.5 mm wide and about 1.5 mm high. The length/width ratio is 1.6–2.5. The profile and ornamentation suggest that they belong to *Acrodus.*

O c c u r r e n c e. — Bone Bed of C unit at Raciborowice. According to Dorka (2001) they are also present in the Upper Triassic of Lower Saxony (Germany). Rieppel (1981) described *Acrodus* teeth from the Middle Triassic of Switzerland. *Acrodus* is also numerous in the Triassic to lower Campanian interval of Europe and Russia (Cappetta, 1987).

Polyacrodontidae Glückman, 1964
Palaeobates Meyer, 1849
Palaeobates angustissimus Agassiz, 1838
(Fig. 4F–I)
MGUWr 5392s–5395s

1973 *Palaeobates angustissimus*, Liszkowski, ryc. 2, fig. 5.
1981 *Palaeobates angustissimus*, Rieppel, figs. 8, 9; fig. 13a–c.
1986 *Palaeobates angusstissimus*, Schultze and Möller, fig. 3c, e.
1987 *Palaeobates angustissimus*, Cappetta, fig. 40 L–N.
1998 *Palaeobates angustissimus*, Chrząstek and Niedźwiedzki, pl. II, fig. 6.
2001 *Palaeobates angustissimus*, Dorka, fig. 1L.
2002 *Palaeobates angustissimus*, Chrząstek, pl. 23, fig. 5.

M a t e r i a l. — Four well-preserved teeth comprise one complete specimen (crown and root), two complete crowns and a half of a crown.

D e s c r i p t i o n. — Teeth are 2–3 mm wide, 5–8 mm long, of rounded margins with a rather low (*ca.* 1 mm) crown. The crown is wider and overhangs the root. The teeth are covered with irregular granulation composed of small oval elevations and hollows.

O c c u r r e n c e. — Bone Bed of unit C at Raciborowice. Chrząstek and Niedźwiedzki (1998) and Chrząstek (2002) described similar teeth from this bed. According to Schmidt (1928) this species occurs in the Upper Roetian and Muschelkalk of Jena (Thuringia, Germany). Liszkowski (1973) observed similar teeth from the Lower Muschelkalk of Wolica (Łukowa Beds). He also mentioned (Liszkowski, 1993) *Palaeobates angustissimus* from the Lower (Gorażdże Beds and Terebratula Beds), Middle and Upper Muschelkalk of the Opole region. The species is particularly numerous in the Wilkowice Beds and Boruszowice Beds. Liszkowski (1993) also reported *Palaeobates angustissimus* from the Roetian and Lower Muschelkalk of the Holy Cross Mts. (Wolica Beds, Wavy Beds and Łukowa Beds) as well as from the Upper Muschelkalk (*Entolium discites* Beds and *Ceratites* Beds). Dorka (2001) discovered such teeth in Lower Saxony (Germany) while Rieppel (1981) found them in the Middle Triassic of Switzerland. Schultze and Möller (1986) described similar specimens from the Middle Muschelkalk of Göttingen (Germany).

Palaeobates sp.
(Figs. 4J and 5A–C)
MGUWr 5396s–5399s

M a t e r i a l. — Two fragmentary and two complete well-preserved teeth.

D e s c r i p t i o n. — The teeth are elongated, measuring 3–5 mm in length, 1.5–3 mm in width and 1–1.5 mm in height. The length/width ratio is 2.25–3.3. Fine striations radiate from the longitudinal ridge, running across the crown (Fig. 5A). The granulation is composed of small irregular, generally oval elevations and hollows an ornamentation typical of *Palaeobates*. It is less characteristic in the specimens (Fig. 5B) where it slightly resembles that of *Acrodus*. The tooth (Fig. 5C) also shows the ornamentation somewhat different from typical one. The crown is characteristically granulated on one side of the longitudinal crest but is covered by folds, in places bifurcating, which run in various directions from the crest on the other side (resembling that of *Acrodus*).

O c c u r r e n c e. — In the North-Sudetic Basin the species occurs in the Bone Bed of unit C. *Palaeobates* was described from the Middle to Upper Triassic in Europe and North America (Cappetta, 1987).

Class: Osteichthyes Huxley, 1880
Subclass: Actinopterygii Klein, 1885
Order: Saurichthyiformes Hay, 1902
Birgeriidae Aldinger, 1937
Birgeria Stensiö, 1919
Birgeria sp.
(Fig. 5D)
MGUWr 5400s

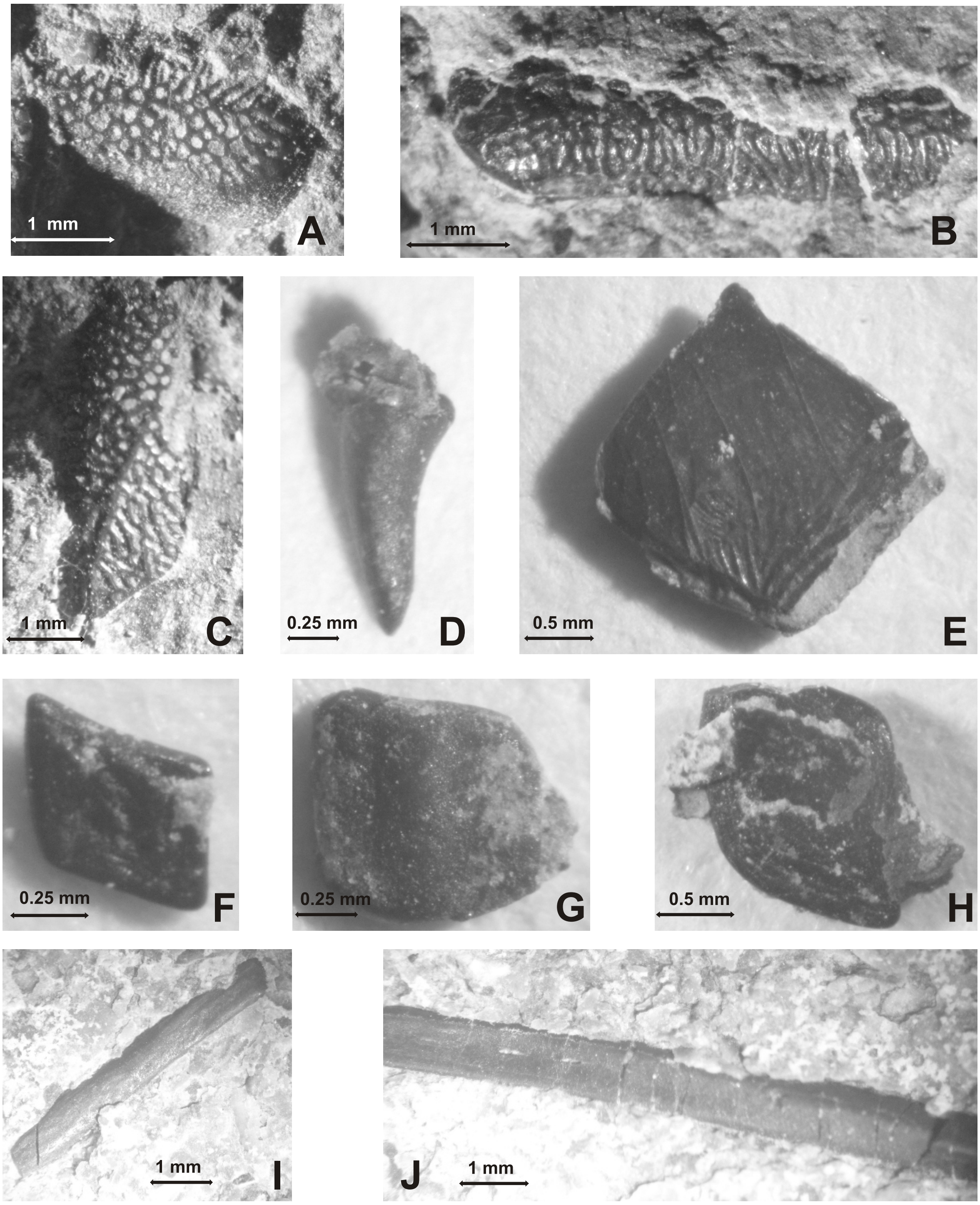

Fig. 5. Fish teeth, scales and bones from the Bone Bed (unit C) of the Lower Muschelkalk at Raciborowice Górne

A–**C** — *Palaeobates* sp.; **D** — *Birgeria* sp.; **E**–**F** — scales of *Gyrolepis* sp.; **G**–**H** — Actinopterygian scales; **I**–**J** — enigmatic bones (fish?)

M a t e r i a l. — One fragmentary but well-preserved tooth.

D e s c r i p t i o n. — The tooth is small, very slightly curved and broad-based. It measures 1.5 mm in length and 0.5 mm in width. The surface is smooth without noticeable ornamentation.

O c c u r r e n c e. — In Raciborowice Górne this species occurs in the Bone Bed of unit C. Vickers-Rich *et al.* (1999) described similar *Birgeria* teeth from the Middle Triassic of Saudi Arabia. They also noted that the species is known from the Early Triassic to Rhaetian and is of wide geographic extent (North America, Greenland, Spitsbergen, Madagascar).

Order: Palaeonisciformes Hay, 1929
Acrolepididae Aldinger, 1937
Gyrolepis Agassiz, 1833
Gyrolepis sp.
(Fig. 5E–F)
MGUWr 5401s; 5402s

M a t e r i a l. — Two complete scales with faint ornamentation.

D e s c r i p t i o n. — The scale are rhomboidal, 0.8 and 2.6 mm across respectivelly. Only one of the specimens shows delicate perpendicular striation.

O c c u r r e n c e. — In the North-Sudetic Basin these scales were described from the Bone Bed of unit C. Liszkowski (1981) discovered teeth belonging to various species of the genus *Gyrolepis* from the Silesia–Kraków region and from the Holy Cross Mts. According to Schultze and Möller (1986) similar specimens occur in the Middle Muschelkalk of Göttingen (Germany).

Scales of Actinopterygii
(Fig. 5G–H)
MGUWr 5403s; 5404s

M a t e r i a l. — Two scales with faint ornamentation.

D e s c r i p t i o n. — Oval and ellipsoidal scales measuring 1.1 mm and 2 mm across. One of them lacks any noticeable ornament (Fig. 5G) while the other shows faint ridges parallel to the edges (Fig. 5H). They do not differ significantly from the scales of *Colobodus* described by Schmidt (1928, fig. 1022a,f–g) but poorly preserved ornamentation hinders a more definite taxonomic assignment.

O c c u r r e n c e. — Bone Bed of unit C at Raciborowice Górne.

Enigmatic bones
(Figs. 5I–J and 6A)
MGUWr 5406s; 5405s-1; 5405s-2

M a t e r i a l. — Three very well preserved specimens.

D e s c r i p t i o n. — One bone has the shape of an inverted letter T and a smooth surface (Fig. 6A). The base is 4–4.5 mm across down to 2 mm at the thinnest section. The specimen measures 5 mm in length. It resembles the skull bone of an actinopterygian fish (Hagdorn, pers. comm.).

Other bones are elongated and measure 0.75 mm and 1 cm in length and about 0.75 mm in width (Fig. 5I–J). Their surface is generally smooth though longitudinal ridges and delicate folds may be observed (Fig. 5I). They resemble fish bones (Hagdorn, pers. comm.).

O c c u r r e n c e. — The Bone Bed of unit C at Raciborowice Górne.

Superclass: Terapoda
Class: Reptilia
Subclass: Euryapsida
Order: Eosauropterygia Rieppel, 1994
Suborder: Eusauropterygia Tschanz, 1989
Infraorder: Nothosauroidea Baur, 1889
Superfamily: Nothosauria Baur, 1889
Nothosauridae Baur, 1889
Nothosaurus Münster, 1834
Nothosaurus cf. *mirabilis*
(Fig. 6J)

M a t e r i a l. — One very well preserved vertebra.

D e s c r i p t i o n. — The roughly square-shaped vertebra of the reptile measures 1.5 2.0 cm. A centrally located pit broadens towards the edges. The specimen does not differ from vertebrae of the reptile *Nothosaurus mirabilis* described by Schmidt (1928, fig. 1112a).

O c c u r r e n c e. — In thick-bedded organodetrital limestone with abundant crinoids of unit B. Similar vertebrae were described from the same horizon by Chrząstek and Niedźwiedzki (1998) and by Chrząstek (2002). Schmidt (1928) noted similar specimens from the Muschelkalk of Germany.

Suborder: Eusaropterygia
(Fig. 6B–D)
MGUWr 5407s–5409s

M a t e r i a l. — Three well-preserved teeth — one complete and two with broken tips.

D e s c r i p t i o n. — The teeth are triangular, slightly curved with longitudinal striation. The specimens measure 0.75, 4 and 6.5 mm in length and 0.3, 1 and 1.5 mm in width. Their profile and ornamentation suggest that they belong to the family Nothosauridae or Cymatosauridae though precise taxonomic attribution is not possible based on isolated teeth only.

O c c u r r e n c e. — For the first time noted at Raciborowice Górne from the Bone Bed of unit C. Reif (1980) found similar teeth at Baden–Würtemberg (SW Germany).

Vertebrate coprolites
(Fig. 6E–J)

M a t e r i a l. — Seven well preserved specimens.

D e s c r i p t i o n. — The specimens are elongated, well rounded. They measure 1.5–2.5 cm in length and 0.5–1.0 cm in width.

O c c u r r e n c e. — In two horizons of organodetrital limestone, one with abundant *Dadocrinus*, the other with numerous *Myophoria vulgaris*, in the lower and upper parts of unit B of the Raciborowice Górne Lower Muschelkalk section, respectively.

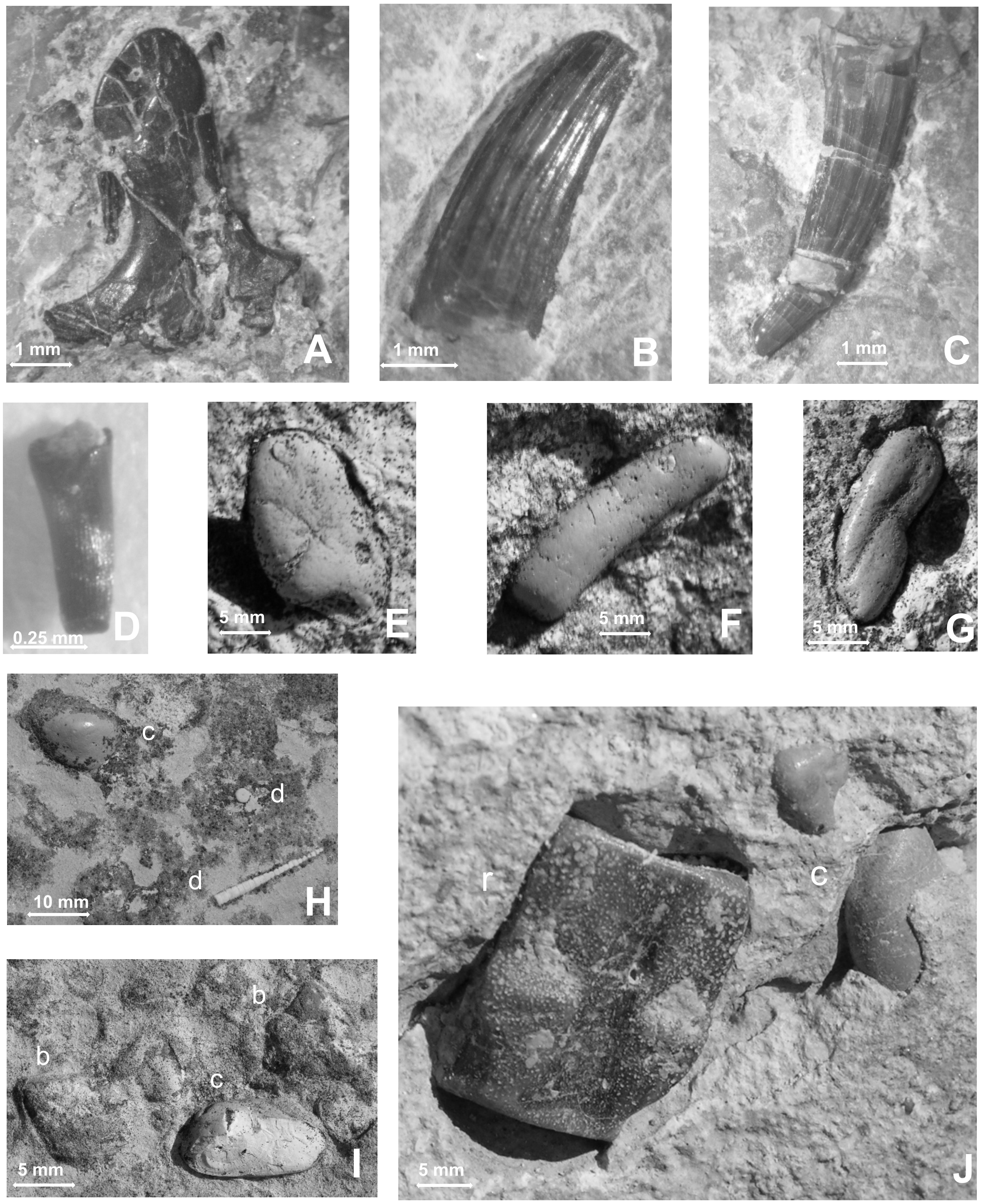

Fig. 6. Vertebrate remains from the Bone Bed of unit C (A–D) and from unit B (E–J) of the Lower Muschelkalk at Raciborowice Górne

A — enigmatic bone (actinopterigian?); **B**–**D** — reptiles teeth (nothosaurids or cymatosaurids); **E**–**G** — coprolites; **H** — c — vertebrate coprolite, d — *Dadocrinus* sp.; **I** — c — vertebrate coprolite, b — bivalves (*Myophoria vulgaris*); **J** — r — vertebra of *Nothosaurus* cf. *mirabilis*, c — vertebrate coprolite

PALAEOENVIRONMENT

The beds of unit B, rich in the remains of vertebrates, mainly reptiles, were deposited in a shallow environment. Water salinity was generally normal marine as shown by a mass occurrence of the crinoids *Dadocrinus* and (less frequent) *Holocrinus acutangulus* (Hagdorn and Głuchowski, 1993; Chrząstek, 2002). However a horizon of cellular limestone (Fig. 2) indicates that periodic sea level changes and episodic emergences took place. Such a type of limestone is typically formed in the sabkha environment (*sensu* Wilson, 1975). Lithological and palaeontological data suggest a lagoon with restricted water circulation as a dominant environment during the deposition of unit B (Chrząstek, 2002). Szulc (1991) proposed similar sedimentary conditions for unit B and interpreted the cellular limestone as a postevaporitic fabric. The domination of bones and vertebrae of reptiles (*Nothosaurus* cf. *mirabilis*) as well as a lack of scales and teeth of fish in the skeletal assemblage seem to support that concept. The reptiles probably lived in a very shallow lagoon.

The assemblage of macro- and ichnofossils present in unit C indicates a somewhat deeper sedimentary environment for these beds (Chrząstek, 2002). Limestones of the unit are dark, pyrite-bearing with the ichnofossil *Planolites* isp. and scarce vertebrate remains that suggest a lower oxygen content in the seawater. Low oxygenation might have been caused by the decomposition of fish remains. Abundant teeth may indicate that sharks were common in the Germanic Basin.

Based on the collected teeth assemblage it may be concluded that during the sedimentation of unit C the shark population was dominated by euryhaline bottom-dwelling selachians that fed on benthos (*Acrodus* sp. and *Palaeobates* sp.). This is indicated by the presence of crushing teeth and frequent layers containing gastropods and bivalves — organisms that constitute a common sclerophages' diet (Fig. 3). Reif (1982) considered "generalized sharks" as contemporary equivalents of the Triassic and Cretaceous sharks. They are rather slow-swimming bottom-dwellers that feed on small fish, thin-shelled bivalves, worms and other benthic organisms. Boss (1982) distinguished 3 types of chondrichthyan teeth and classified the Triassic assemblage as of type I, i.e. teeth adapted for crushing shells. According to him a Triassic chondrichthyan had an elongated body and large mouth to prey on larger organisms. Scales and teeth of osteichthyans are less numerous, which may suggest that the Sudetic basin was too shallow for them.

Bürgin (1999) reported vertebrate remains from lithologically similar dark-grey limestone in the Lower Muschelkalk of southern Switzerland (Monte San Giorgio). According to him the limestone was formed in the anoxic environment of a shallow lagoon.

Thus the sedimentary environment of unit C was shallow but somewhat deeper than the one of unit B (Szulc 1991; Chrząstek, 2002). The analysis of ichnoassociations (Chrząstek, 2007) indicates that the part of unit C containing the Bone Bed shows a regressive trend. This is shown by the presence of hardground intraclasts in the *Spiriferina* Bed that occur a little higher in the section. The break in sedimentation, as shown by hardground formation, may be related to transgressive-regressive events (Chrząstek, 2004). The maximum marine transgression in the studied region, caused probably by the opening of the Silesian-Moravian marine gateway, started immediately with the deposition of the *Spiriferina* Bed (Kędzierski and Szulc, 1996; Chrząstek, 2002). It may be concluded that the sedimentary environment of the Lower Muschelkalk deepened gradually from the beginning of unit B deposition. The basin reached its maximum depth during the sedimentation of the upper part of unit C and unit E. This is confirmed by the assemblage of macro- and ichnofossils (Fig. 3; Chrząstek, 2002, 2007).

CORRELATION

Palaeontological data on vertebrates from the Lower Muschelkalk showed that fish remains are common in the Germanic Basin (Central Europe), including Poland. According to Liszkowski (1981) the vertebrate remains are represented mainly by isolated fragments of external (scales, fin rays) and internal (vertebrae, teeth) skeleton. This is supported by the assemblage of vertebrate fossils from the Lower Muschelkalk at Raciborowice Górne where numerous isolated teeth, sporadic scales, bones of reptiles and probably of fish were discovered. The collected vertebrate remains from the North-Sudetic Basin shows a great similarity to the age-equivalent assemblage from Wolica near Chęciny in the Holy Cross Mts. (Liszkowski, 1973, 1981, 1993). It occurs in the Łukowa Beds, in the Lower Muschelkalk section of the Holy Cross Mts., an equivalent of unit C of the North-Sudetic Basin (Głuchowski and Salamon, 2005). Although the fauna from the Holy Cross Mts. is richer in taxa, similar chondrichthyans (*Acrodus lateralis*, *Acrodus* sp., *Palaeobates angustissimus* and *Palaeobates* sp.) and osteichthyans (*Birgeria* sp. and *Gyrolepis* sp.) occur in both regions.

The skeletal remains from the Lower Muschelkalk of Raciborowice Górne are also similar to the age-equivalent assemblages from the Gogolin Beds of the Upper Silesia. The latter are dominated by *Hybodus* sp., *Acrodus lateralis*, *Palaeobates* sp. and *Lissodus* sp. with less common *Polyacrodus* sp. (Liszkowski, 1981, 1993). Osteichthyans — *Saurichthys* sp., *Colobodus* sp. and *Gyrolepis* sp. — also occur (Liszkowski, 1981). Thus the Sudetic assemblage is comparable to both of these age-equivalent faunas though it most closely resembles the assemblage from the Holy Cross Mts. As in the North-Sudetic Basin the maximum abundances of such taxa as *Acrodus lateralis* and *Palaeobates angustissimus* were observed in the Łukowa Beds, an equivalent of unit C at Raciborowice Górne.

In Lower Silesia, Upper Silesia and in the Holy Cross Mts. chondrichthyan teeth dominate (mostly *Acrodus* sp. and *Palaeobates* sp.) while teeth and scales of Actinopterygii are rare. On the other hand *Hybodus* sp., *Lissodus* sp., *Polyacrodus* sp. and *Saurichthys* sp., present in the Holy Cross Mts. and in the Silesia-Kraków region, were not observed in the North-Sudetic Basin.

The taxonomic composition of the skeletal remains from the Lower Muschelkalk of Raciborowice Górne shows also many similarities to the equivalent faunas from other regions of Europe. It does not differ from the German assemblage that includes such fish taxa as: *Acrodus* sp., *Hybodus* sp., *Palaeobates* sp., *Gyrolepis* sp., *Saurichthys* sp. (Reif, 1980; Kriwet and Schultz, 1998; Bürgin, 1999). Similar Chondrichthyes and Osteichthyes are known from the Middle Triassic of the Netherland: *Acrodus* sp., *Palaeobates angustissimuss*, *Gyrolepis* sp., *Colobodus* sp., *Saurichthys* sp. and *Birgeria* sp., France: *Gyrolepis* sp., *Saurichthys* sp., *Birgeria* sp. and *Colobodus* sp. as well as northern Italy: *Acrodus* sp., *Hybodus* sp., *Saurichthys* sp. and *Colobodus* sp. (Bürgin, 1999). In the Triassic of north-eastern Spain chondrichthyans do not occur but osteichthyan remains such as *Saurichthys* sp. and *Colobodus* sp. are common

(Beltan, 1972 in Bürgin, 1999). Birkenmajer and Jerzmańska (1979) described similar taxa: *Hybodus* sp., *Acrodus* sp., *Polyacrodus* sp. and *Saurichthys* sp. from the Lower Triassic of Spitsbergen. *Hybodus* sp., *Gyrolepis* sp. and *Lissodus* sp. were on the other hand noted from the Upper Triassic of Luxembourg (Godefroit *et al*., 1998).

Describing the teeth of Chondrichthyes and Actinopterygii from the Middle Triassic of southern Switzerland, Bürgin (1999) reported *Gyrolepis* sp. and *Acrodus* sp., which occur also at Raciborowice Górne. The difference between the Sudetic assemblage and its Swiss age equivalent lies in a greater number of actinopterygian taxa in the latter. Rieppel (1981) also mentioned *Hybodus* sp., *Acrodus lateralis* and *Palaeobates angustissmus* from the Middle Triassic of southern Switzerland.

According to Minikh (1998) many Triassic vertebrates occur also in the age-equivalent deposits of Russia (*Hybodus* sp., *Acrodus* sp., *Lissodus* sp., *Ceratodus* sp., *Saurichthys* sp., *Colobodus* sp.).

The taxonomic composition of the assemblage of fish remains from the Lower Muschelkalk of the North-Sudetic Basin does not differ significantly from the faunas of the Germanic facies from other regions of Poland (Holy Cross Mts., Silesia–Kraków region) and the rest of Europe: Germany, the Netherlands and Luxembourg. It is also similar to the Alpine facies assemblages of the same age, though osteichthyan taxa are considerably less numerous in the Lower Muschelkalk of the North-Sudetic Basin compared to the assemblages known from Switzerland, Austria and northern Italy (Bürgin, 1999). These sharks preferred probably deeper environments and the Sudetic Basin was too shallow. Consequently Osteichthyes, especially Actinopterygii, dominated and taxonomically more diverse in the Tethys Ocean. The assemblages of vertebrate remains from the epicontinental basins of Spain and France, located closer to the Tethys Ocean, also differ from those from the Germanic Basin. They are richer in Osteichthyes but poorer in, or lack completely, Chondrichthyes taxa. Similar conclusion may be drawn from the analysis of taxonomic diversity of vertebrate remains in the Lower Muschelkalk of Russia. Apart from chondrichthyans, typical of the Triassic, the number of osteichthyan genera and species is significant.

PALAEOGEOGRAPHY

According to Kriwet and Schultz (1998) the migration of Chondrichthyes and Osteichthyes: *Acrodus* sp., *Hybodus* sp., *Palaeobates* sp. and *Saurichthys* sp. from the Tethys Ocean through the East Carpathian marine gateway into the Germanic Basin took place in the late Scythian. In the early Anisian (Roetian/Muschelkalk) *Chondrichthyes*: *Acrodus* sp., *Hybodus* sp., *Palaeobates* sp., *Polyacrodus* sp. and *Lissodus* sp. became widespread across the entire shallow Germanic Basin. This is linked to a transgression from the Tethys Ocean through the Silesian–Moravian and East Carpathian marine gateways towards northern Germany into the southern part of the North Sea as well as south-westwards to Burgundy. Some of the osteichthyan taxa, such as: *Saurichthys* sp., *Colobodus* sp., *Gyrolepis* sp. and *Birgeria* sp., reached the Germanic Basin though they dominate clearly in the Alpine Basin (Austria, Switzerland) and in other epicontinental basins located close to the Tethys Ocean (Spain, France).

According to Minikh (1998) a connection between the Russian Basin and the Boreal and Tethys oceans existed in the Anisian. The Middle Triassic transgression spread out towards the Urals resulting in the domination of Osteichthyes over Chondrichthyes taxa in the Russian Triassic deposits, as in the Alpine sequences.

Rieppel and Hadgorn (1997), based on the analysis of reptiles distribution, proposed that sauropterygians migrated from the Asiatic Province into the Germanic Basin through the Silesian–Moravian marine gateway. They suggested this direction of transgression because *Nothosaurus* sp. did not appear in the Alpine Triassic until the Anisian/Ladinian, when the western marine gateway opened.

Assemblages of skeletal remains in the North-Sudetic Basin and in the remaining part of the Germanic Basin are similar. Thus they do not offer a sufficient basis to conclude whether the East Carpathian or the Silesian–Moravian marine gateway was the dominant connection with the Tethys Ocean. In the late Olenekian and early Anisian (*sensu* Nawrocki and Szulc, 2000) faunal migration took place most likely through both gateways as suggested already by Szulc (2000) and Niedźwiedzki and Salamon (2002). The Silesian–Moravian marine gateway became dominant from the deposition of the *Spiriferina* Bed, when the brachiopod *Punctospirella fragilis* and numerous crinoids and ammonites appeared in the North-Sudetic Basin (Chrząstek, 2002). At that time the Sudetic Basin started to deepen considerably, which may be related to the existence of a convenient connection with the Tethys Ocean probably through the Silesian–Moravian marine gateway (Kędzierski and Szulc, 1996; Chrząstek, 2002). The data of Głuchowski and Salamon (2005) suggest that this event could take place at the beginning of the Pelsonian. The position of the Bone Bed about 4.5 m below the *Spiriferina* Bed in unit C of the section may indicate its early Anisian (Bithynian) age.

SUMMARY AND CONCLUSIONS

Five taxa of chondrichthyan and, for the first time, two taxa of osteichthyan fishes (Table 1) were found in the Lower Muschelkalk of the North-Sudetic Basin. Vertebrate bones (fishes?, reptiles) and, not hitherto records from Raciborowice Górne, teeth of the reptiles Nothosauroidea or Cymatosauroidea were also recovered.

Reptile remains are present mostly in unit B while fish teeth occur in a characteristic dark grey pyrite-bearing limestone layer (Bone Bed) about 4.5 m below the *Spiriferina* Bed of unit C. Apart from fish teeth that had been already described, the Bone Bed contains also enigmatic bones (fish?) and teeth from nothosaurids or cymatosaurids.

The Sudetic assemblage is composed mainly of teeth belonging to Chondrichthyes whereas Osteichthyes are rare. The assemblage is typical of the Lower Muschelkalk, in which euryhaline bottom-dwelling selachians that fed on benthos prevailed. Layers containing gastropods and bivalves are common in the profile and indicate that prey was easily available. According to Reif (1982) the so-called "generalized sharks" may be contemporary equivalents of the Triassic and Cretaceous selachians that living in a similar habitat.

During the sedimentation of the Bone Bed, the environment was oxygen-deficient as shown by dark colour of the limestone, the presence of pyrite mineralization and the ichnofossil *Planolites* isp. The seawater probably had a low oxygen content because of large quantity of decomposing chondrichthyans that constituted a source of numerous teeth.

The transgression developed from the beginning of the Lower Muschelkalk. Unit B formed in the shallower environment of a lagoon with restricted water circulation (Chrząstek, 2002). Unit C, on the other hand, was deposited in a deeper lagoon with less restricted water circulation (Chrząstek, 2002). This is also indicated by the assemblage of reptile bones (unit B) as well as of chondrichthyan and osteichthyan teeth (unit C).

The Sudetic assemblage shows the closest similarity to that of the age-equivalent strata from the Holy Cross Mts. As an assemblage typical of the Germanic Basin it does not differ significantly from the faunas of the same age from other regions of Poland (Upper Silesia), Germany, France, the Netherlands, Spain, northern Italy, Austria, Switzerland and Russia. It should be noted, however, that the Alpine facies faunas (Austria, Switzerland) consist mostly of osteichthyan remains. A similar situation is observed in the assemblages from epicontinental seas located close to the Tethyan Ocean, i.e. in Spain and France. It may be suggested that these fishes preferred deeper environments whereas the Sudetic and maybe also the Germanic Basins were too shallow.

From the late Olenekian to the early Anisian, during the sedimentation of the vertebrate-bearing units B and C, a connection with the Tethyan Ocean ran through the East Carpathian and Silesian–Moravian marine gateways as suggested already by Szulc (2000) and Niedźwiedzki and Salamon (2002). The Silesian–Moravian marine gateway became more important during the sedimentation of the *Spiriferina* Bed. Significant deepening of the basin suggests a good connection with the Tethyan Ocean at that time. This is supported by the palaeontological record of this part of unit C (Chrząstek, 2002; 2007).

Głuchowski and Salamon (2005) suggested a Pelsonian age for the *Spiriferina* Bed. This indicates an early Anisian (Bithynian) age for the Bone Bed because it occurs about 4.5 m below the *Spiriferina* Bed in the Lower Muschelkalk section.

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