

DIVERSITY OF VERTEBRATE REMAINS FROM THE LOWER GOGOLIN BEDS (ANISIAN) OF SOUTHERN POLAND

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Abstract: Middle Triassic (Muschelkalk) limestones and dolostones of southern Poland contain vertebrate remains, which can be used for palaeoecological and palaeogeographical analyses. The results presented concern vertebrate remains uncovered at four localities in Upper Silesia and one on Opole Silesia, a region representing the south-eastern margin of the Germanic Basin in Middle Triassic times. The most abundant remains in this assemblage are fish remains, comprising mostly actinopterygian teeth and scales. Chondrichthyan and sauropsid remains are less common. Reptilian finds include vertebrae, teeth and fragments of long bones, belonging to aquatic or semi-aquatic reptiles, such as nothosaurids, pachypleurosaurids, and ichthyosaurids. Also, coprolites of possibly durophagous and predacious reptiles occur. In the stratigraphic column of Mikołów, actinopterygian remains are the most numerous and no distinct changes of the taxonomic composition occur. Although this assemblage differs from those described at other localities (Ząbkowice with numerous chondrichthyans, Żyglin, and Płaza with common sauropsid fossils), sampling bias has to be considered.

Key words: Chondrichthyes, Actinopterygii, Reptilia, fossil vertebrate, tempestite, coprolite, Middle Triassic.

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INTRODUCTION

The bone remains and coprolites of Middle Triassic marine vertebrates are well known from many localities in Europe (e.g., Rieppel and Hagdorn, 1998; Stockar, 2010; Diedrich, 2012; Voeten *et al.*, 2014; Brachaniec *et al.*, 2015; Klein *et al.*, 2015) and Asia (e.g., Jiang *et al.*, 2009; Benton *et al.*, 2013), which correspond to the areas of the Germanic Basin and eastern Tethys, respectively. These animals emerged from the most devastating biota crisis in the Earth's history, the P-T extinction event (PTEE) that completely remodelled both marine and terrestrial ecosystems. There are two competing hypotheses of the exact dynamics of the post-extinction biota re-establishment. One of them assumes that the biotic recovery was prolonged and gradual, accelerating only in the late Early and early Middle Triassic, which could have been caused by repeated environmental disturbances, lasting till 5–6 Myr after the PTEE (Chen and Benton, 2012; Benton *et al.*, 2013). The second one, on the other hand, claims that the recovery was rapid, with the appearance of multitrophic webs already at the beginning of

the Early Triassic (Scheyer *et al.*, 2014). In either case, as a result of these profound changes, new groups of animals started to dominate marine environments, including the animals, which took over the ecological niches that had never been occupied before (Benton *et al.*, 2013). This included the first major radiation of marine reptiles, such as the thalattosaurs, sauropterygians (nothosaurs, pachypleurosaurids, and placodonts) and ichthyopterygians (Rieppel, 2000; Benton *et al.*, 2013). Fishes (especially actinopterygians) also started to radiate. However, some of the Palaeozoic representatives persisted throughout the Triassic or even the entire Mesozoic, e.g., Palaeoniscidae.

Following the vertebrate evolution during the Lower-Middle Triassic, therefore, is essential for the proper understanding of the impact of the PTEE on life and the dynamics of post-extinction ecological and evolutionary changes. One of the places, which may provide this information is the Silesia region (both Lower and Upper Silesia) in southern Poland, which was located in the south-eastern part of the Germanic

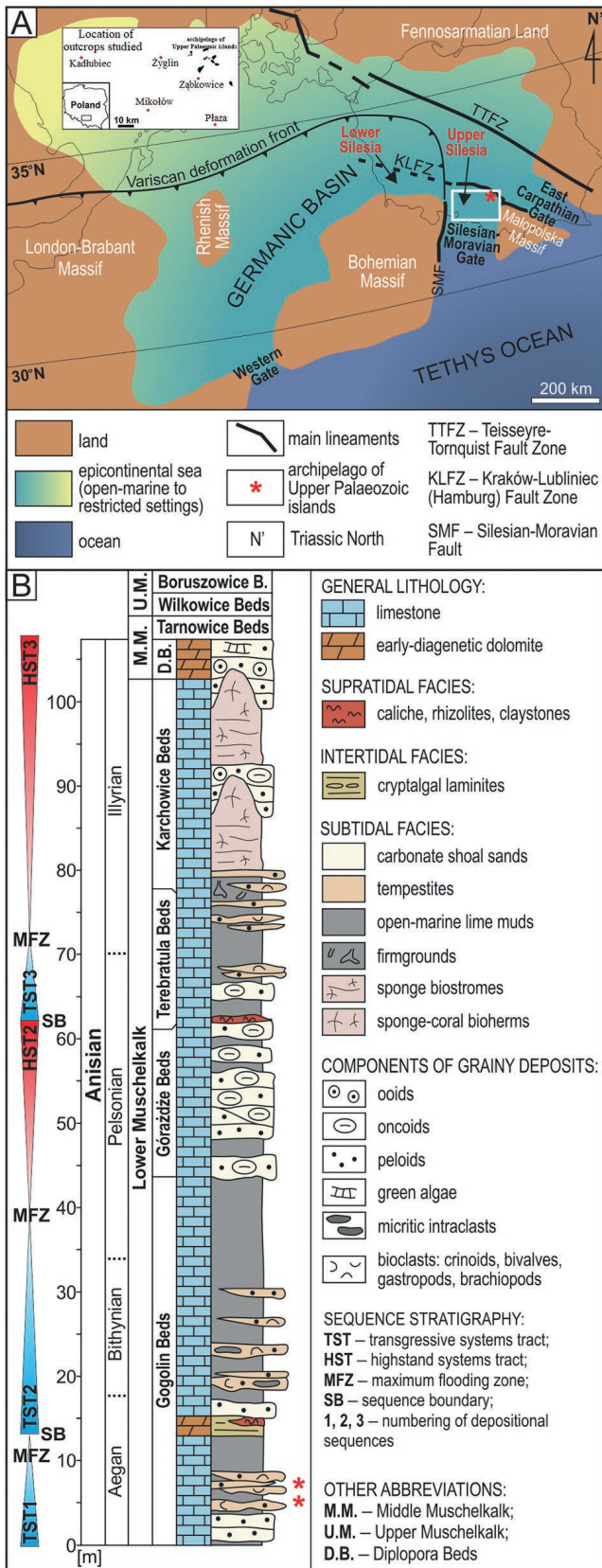


Fig. 1. Palaeogeography and lithostratigraphy of Silesia. **A.** Palaeogeographic position of the Upper Silesia study region (white rectangle), close to the Tethys Ocean (modified from Szulc, 2000). **B.** Generalised lithostratigraphic column for the Muschelkalk of the Upper Silesia study region after Matysik (2014 and references cited herein). Levels, from which the studied fossil specimens were obtained, are indicated by red asterisks.

Basin, close to the Tethys Ocean (Fig. 1A). Here, numerous vertebrate remains have been found in the uppermost Lower and Middle Triassic marine carbonates for almost 200 years (e.g., Meyer, 1849; Eck, 1865; Roemer, 1870; Langenhan, 1911; Schmidt, 1928, 1938; Śliwiński, 1964; Sander and Mazin, 1993; Chrzastek and Niedźwiedzki, 1998; Hagdorn and Rieppel, 1999; Chrzastek, 2008; Surmik, 2010; Surmik and Brachaniec, 2013; Matysik and Surmik, 2016; Wintrich *et al.*, 2017). However, broad descriptions of the Silesian vertebrate assemblages and more detailed descriptions of individual bones are rare in the literature (Chrzastek and Niedźwiedzki, 1998; Surmik, 2010; Surmik and Brachaniec, 2013; Wintrich *et al.*, 2017).

The aim of this paper is to test the stratigraphic variability of vertebrate assemblages within the lowermost part of Middle Triassic (Anisian) deposits, called the Lower Gogolin Beds (Fig. 2), by means of the detailed, bed-by-bed description of vertebrate remains in a continuous section at Mikołów and their comparison with findings at other localities, including Płaza, Żyglin, and Ząbkowice. Such stratigraphic changes (or the lack of them) might be a premise for inferring the evolution of marine ecosystems in the early Middle Triassic. The article also provides new fossil material, belonging to taxa poorly represented and described from the discussed area, and an update on the occurrences of the specific taxa at some of the sites investigated.

GEOLOGICAL SETTING

In the Middle Triassic, the Upper Silesia study region was located at the northern outlet of the Silesian-Moravian Gate, one of the three submeridional seaways, connecting the Tethys Ocean to the south with the semi-closed, subtropical Germanic Basin to the north (Szulc, 2000). The region itself was bounded to the west by the Bohemian Massif and to the east by the Małopolska Massif and an archipelago of several, cliff-edged Devonian islands (Fig. 1A).

The depositional record in the region was strongly controlled by the superimposed, long-term, tectonic evolution of the adjacent gate, third-order to higher-rank, relative sea-level oscillations and platform morphology (Szulc, 2000; Matysik, 2014, 2016, 2019). The Lower Muschelkalk represents the maximum opening of the neighbouring gate. It encompasses deposits 100 m thick, dominated by open-marine limestones, which evolved from ramp tempestites and fair-weather lime muds (Gogolin Beds) to flat-bank calcareous sands (Górażdże Beds), to a rimmed platform with fore-barrier sponge-coral patch reefs (Karchowice Beds) and back-barrier, lagoonal dolomitic facies (Diplopora Beds). In contrast, the Middle and Upper Muschelkalk formed during the tectonic uplift of the area and consequently reach only 50 m in thickness and essentially are composed of the restricted dolomitic (Diplopora and Tarnowice Beds) and siliciclastic (Boruszowice Beds) facies of a marginal sea (Fig. 1B).

The bone-rich beds occur in the Gogolin Beds dominated by nodular and wavy-bedded lime mudstones, with less common crinoid-shelly wackestone-packstone coquinas (tempestites) and peloid-oid-oncoid grainstones-packstones (shoal sands). The sediments overall are strongly

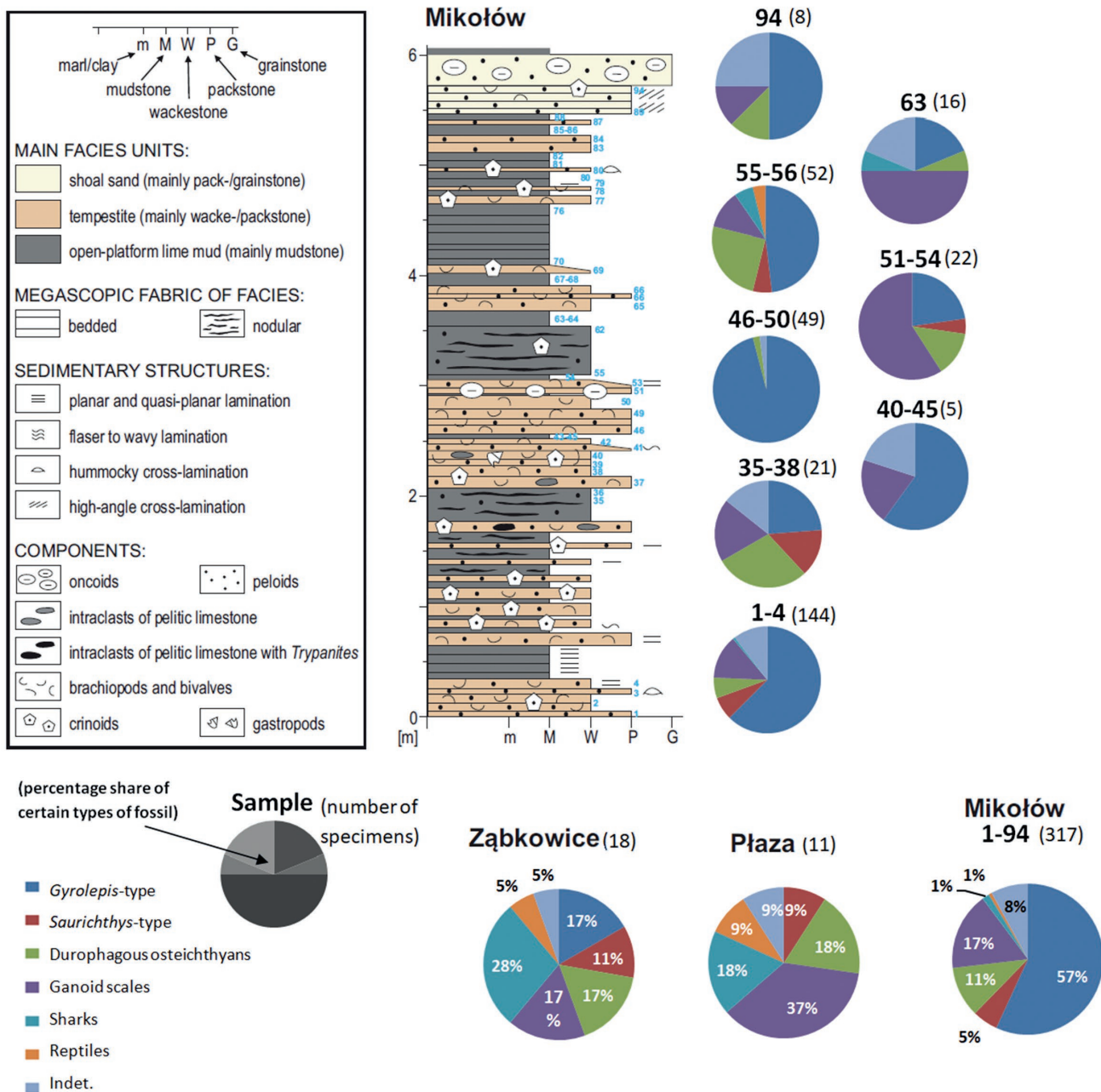


Fig. 2. Lithostratigraphic column of the Lower Gogolin Beds in Mikołów and the percentage share of fossils of several groups in dissolved samples from Mikołów (INGUJ214P/Mik/1–94), Ząbkowice (INGUJ214P/Zab/0), and Płaza (INGUJ214P/P/0).

bioturbated and contain numerous, moderately diversified, invertebrate trace fossils, mostly of polychaetes (Stachacz and Matysik, 2020).

MATERIAL AND METHODS

The material analysed comprises micro- and macrofossils from Mikołów, Płaza, Żyglin, and Ząbkowice, and several coprolites from Kadłubiec. All specimens are housed at the Jagiellonian University in Kraków and labelled: INGUJ214P/Mik/1–94, INGUJ214P/Zy/1–11, INGUJ214P/Kad/1–3, INGUJ214P/Zab/0, INGUJ214P/P/0–7.

Microfossils were prepared using the following methods and techniques, described by Sibert *et al.* (2017). The rock

samples were fragmented and dissolved in a 10% acetic acid solution under a fume hood with regular acid renewal every 24 hours. After decantation of the acid, the dissolved sediment was washed in distillate water and sieved to separate the different fractions. The residuum obtained was subsequently observed under a stereomicroscope to hand-pick the fossils. Photographs of the specimens were taken, using a Leica M165C binocular lens, equipped with a Leica DFC295 camera. Rock samples before dissolution weighed from 0.1 to 0.5 kg. The lower half of the Lower Gogolin Beds at Mikołów was sampled bed by bed to test the stratigraphical diversity. Samples of single, bone-rich layers from the other localities were dissolved for the geographical comparison.

Coprolites were observed under a binocular and thin sections were made to reveal their internal composition, including the presence of bone and skeletal fragments. A Nikon Eclipse petrographic microscope, equipped with a Nikon D40 camera, was used to take thin-section photographs.

RESULTS

The five studied localities significantly differ with respect to the composition of vertebrate assemblages. At Mikołów, where the Lower Gogolin Beds were sampled bed-by-bed from a profile of sediments, 6 m thick (Fig. 2), individual beds differ in the number of microfossils and the number of fossil types. Throughout the entire profile, the remains of actinopterygians, mostly *Gyrolepis*-like teeth (~59% of all findings), are the most common. In several beds, scales were more numerous than teeth (~59% in beds 51–54 and ~50% in bed 63). Chondrichthyans and reptiles are relatively rare (~1% of all findings).

In the samples from Ząbkowice, chondrichthyan remains (including hybodontid spines and teeth) occur commonly along with the actinopterygians (~27%, in contrast to less than 10% at Mikołów). At the Płaza and Żyglin localities, reptiles (sauroptrygians and ichthyopterygians) that are rarely seen at Mikołów occur. At the Kadłubiec outcrop, only several coprolite specimens were found (Tab. 1).

Shark remains are known to be an important component of numerous Middle and Upper Triassic sites (Böttcher, 2015; Nordén *et al.*, 2015; Slater *et al.*, 2016; Landon *et al.*, 2017; Cavicchini *et al.*, 2018), including some of the Polish localities (e.g., Liszkowski, 1993; Chrzastek and Niedźwiedzki, 1998; Szulc, 2007; Chrzastek, 2008; Kardynał *et al.*, 2016).

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Euselachii Hay, 1902
Superfamily Hybodontoidea Zangler, 1981

Description: Hybodontid fin spines can be found as both micro- and macrofossil remains. They are elongated, slightly recurved, laterally flattened and with distinct, vertical grooves and ridges, extending through the entire length of the specimens, coarsely grooved in the distal part. Larger specimens from Ząbkowice (Fig. 3A) and Żyglin (Fig. 3B) are incomplete distal parts. The microspecimen from Ząbkowice (Fig. 3C) is a small (<2 mm) fragment of the spine.

Two specimens of a placoidal scale were collected (Fig. 3D). The fossils possess a delicate groove and ridge ornamentation both on the base and the crown. A flattened dorsal surface extends posteriorly. These isolated denticles cannot be assigned to a particular taxon because shark

Table 1

Taxonomic composition of vertebrate remains in analysed locations.

	Osteichthyes					Chondrichthyes				Sauropsida		
	<i>Gyrolepis</i>	<i>Severnichthys</i>	<i>durophagous</i>	indet. osteichthyans	scales	<i>Hybodus</i>	<i>Acrodus</i>	<i>Lissodus</i>	indet. chondrichthyans	Nothosauridae	Ichthosauria	indet. sauropsids
Mikołów	x	x	x	x	x	x		?	x			x
Ząbkowice	x	x	x	x	x	x		x	x	x		
Płaza		x	x	x	x		x			?	x	x
Żyglin									x	x		x

SYSTEMATIC PALAEONTOLOGY

The following systematic description is subdivided into fish remains and sauropsid fossils. The taxonomic revision describes all samples analysed, whereas Figures 3–8 illustrate the most representative specimens.

Chondrichthyes

Among the fish remains, a few were identified as belonging to Chondrichthyans, namely hybodontid sharks. The collection consists of placoidal scales, fin spines, and teeth.

scales may have differences in morphology, depending on the ontogenetic stages of a specimen and localization on the fish body (Duffin, 1999; Landon *et al.*, 2017).

Family Lonchidiidae Herman, 1977
Genus cf. *Lissodus* Brough, 1935

Description: One incomplete tooth, lacking a root and part of the crown was collected. It is low and smooth, with a pronounced bulge on the occlusal surface and a flat labial surface. The longitudinal ridge (occlusal crest) extends mesiodistally throughout the distal part of the crown (Fig. 3E).

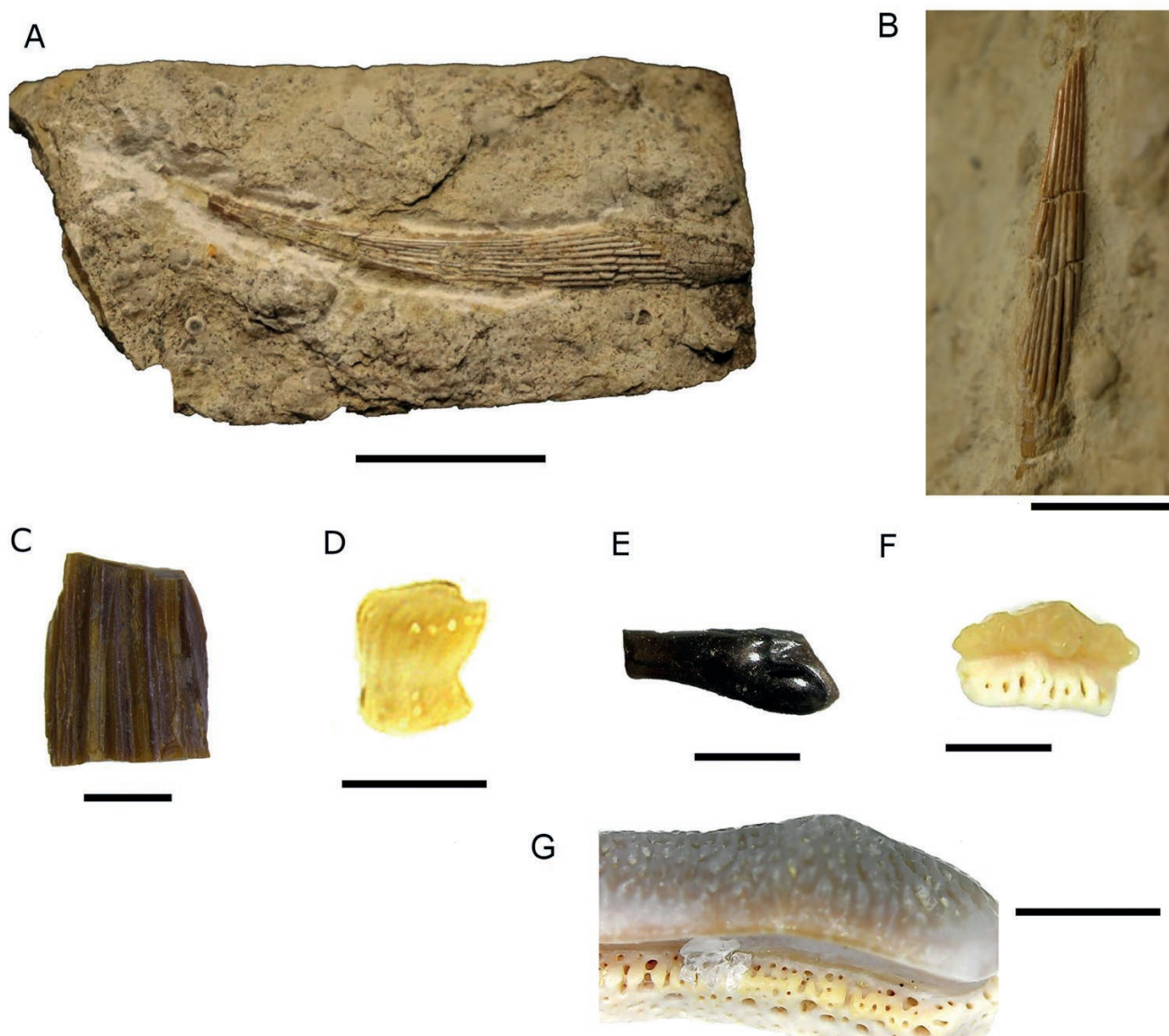


Fig. 3. Chondrichthyes remains from the Lower Gogolin Beds (A, C–E – Żąbkowice, INGUJ214P/Zab/0; B – Żyglin, INGUJ214P/Zy/1; F – Mikołów, INGUJ214P/Mik/55–60; G – Płaza, INGUJ214P/Pl/0). **A, B.** Almost complete hybodontid fin spines, scale bars: 10 mm. **C.** Fragment of hybodontid fin spine, scale bar: 10 mm. **D.** Placoidal scale, scale bar: 0.5 mm. **E.** cf. *Lissodus* fragment of tooth crown, scale bar: 10 mm. **F.** *Hybodus* tooth, scale bar: 0.5 mm. **G.** *Acrodus* tooth, scale bar: 2 mm.

Family Hybodontidae Agassiz, 1843
Genus *Hybodus* Agassiz, 1837

Description: A multicusped tooth with a relatively high base of the crown, larger central cusp, and smaller lateral cusplets. The central cusp is pronounced and has longitudinal striations extending from the base of the cusp to its apex. The cusplets have no clear borders and show a rather gradual change in size (Fig. 3F).

Family Acrodontidae Casier, 1959
Genus *Acrodus* Agassiz, 1838

Description: Tooth is larger than other chondrichthyan remains (Fig. 3G). The tooth is wide but narrow, with an

extensive base and a low, flat crown (~6 mm x 2 mm). The central area of the crown slightly raised, forming a subtle, rounded cusp. The crown is covered with a groove-ridge ornamentation, forming slightly rounded, irregular polyhedral or elongated pits. The slightly more pronounced, but still subtle ridge extends transversally throughout the medial part of the crown.

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Cope, 1872

Remark: Actinopterygian remains are represented by isolated teeth with characteristic transparent tips, isolated ganoid scales, and rare jaw fragments.

Clade Neopterygii Regan, 1923|

Clade Teleosteoromorpha Arratia *et al.*, 2004

Order Semionotiformes Arambourg and Bertin, 1958

Family Macrosemiidae Thiollière, 1858

Description: All ganoid scales are rhomboidal, lacking peg and socket articulation elements. Nonetheless, they can be divided into at least two morphotypes. Morphotype 1 has distinct vertices, a serration on one of the edges, and stair-like notches on the internal surface (Fig. 4A) similar to scales of macrosemiidae (Arratia and Schultzze, 2012). Morphotype 2 is smooth with growth structures (similar to growth rings of cycloid scales) visible on the external surfaces (Fig. 4B) resembling post-anal scales of teleosteoromorphs (Giordano *et al.*, 2016). The presented types might belong to different taxa (Märss, 2006; Antczak and Bodzioch, 2018), but they can also belong to one species, depending on the variability of its structure at different parts of the fish body (Patterson *et al.*, 2002).

Two jaw fragments were found. The first jaw fragment has two oval attachment surfaces (Fig. 4C), characteristic of actinopterygian fishes, specifically being similar to, e.g., bowfin dentaries (DeMar, 2012). The second one represents

a dentary bone with five larger teeth along the ventral edge and several smaller and one large inside the jaw. The bone is perforated with numerous foramina. The teeth possess flattened (or worn) crowns. The innermost (large) tooth is bulbous in shape.

Order Palaeonisciformes Hay, 1902

Family Palaeoniscidae Vogt, 1852

Genus *Gyrolepis* Agassiz, 1843

Description: Teeth are small (up to 0.6 mm long), narrow, and recurved teeth or smooth, conical teeth with narrowed, translucent apices (Fig. 4D). Similar teeth, assigned to the genus *Gyrolepis*, have been frequently found in Röt and Muschelkalk sediments of Upper Silesia since early 20th century (e.g., Assmann, 1933; Kardynał *et al.*, 2016).

Genus *Severnichthys* Storrs, 1994

Description: Several teeth, usually of a relatively large size (0.8–3 mm), can be assigned to genus *Severnichthys* and divided into two morphotypes. The teeth with a

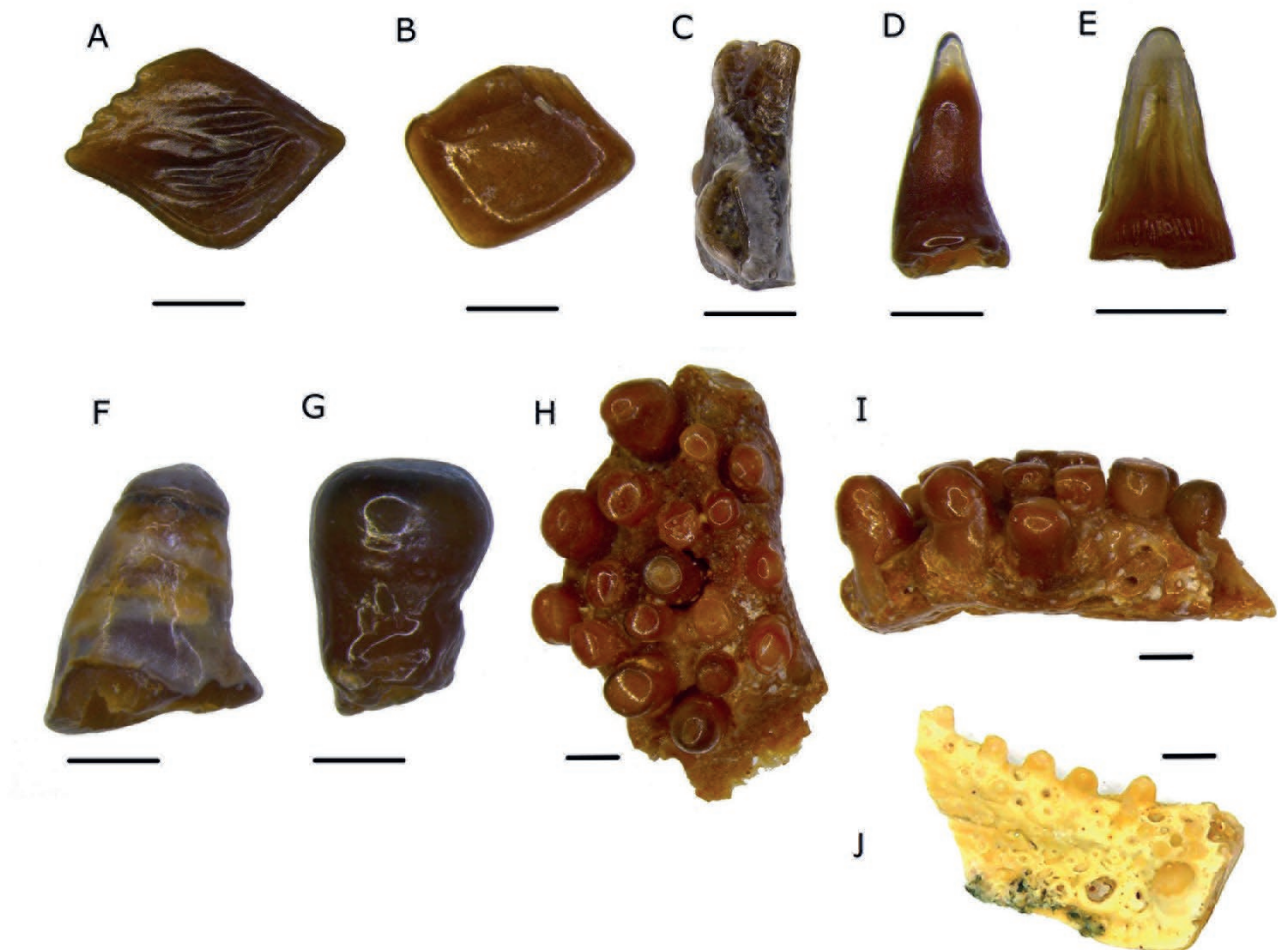


Fig. 4. Osteichthyes remains from the Lower Gogolin Beds in Ząbkowice (A–G, INGJ214P/Zab/0), Mikołów (J, INGJ214P/Mik/55–60) and Płaza (H–I, INGJ214P/Pl/1–2). **A.** Macrosemiidae ganoid scale. **B.** Teleosteoromorpha ganoid scale. **C.** Actinopterygii indet. jaw fragment. **D.** *Gyrolepis* tooth. **E.** *Severnichthys* tooth. **F. G.** cf. *Colobodus* tooth, **H, I.** cf. *Colobodus* tooth plate. **J.** Jaw fragment. All scale bars: 0.5 mm.

smooth, translucent, conical apices, and pronounced vertically rigged bases resemble the *Saurichtyes longidens*-type, whereas pyramidal teeth with a vertical ornament occurring also on the apex more closely resemble *Birgeria mougeoti*-type (Fig. 4F). Both types are known from many Triassic strata worldwide, e.g., Ladinian deposits of southern Hungary (Botfalvai *et al.*, 2019) or Rhaetian deposits of the Stoke Gifford area (Nordén *et al.*, 2015; Landon *et al.*, 2017; Cavicchi *et al.*, 2018).

Order Perleidiformes Berg, 1937
Family Colobodontidae Andersson, 1916
Genus cf. *Colobodus* Agassiz, 1843

Description: Two types of durophagous fish teeth were found. The first type is rounded, slightly longitudinally extended, having a triangular-shaped tooth crown. (Fig. 4F). The second type is bulbous with a flattened occlusal surface of the crown, sometimes bearing radial striations that go downwards from the abraded tip to the root of the tooth (Fig. 4G). As teeth lack any diagnostic features, their assignment to a specific taxon is uncertain. However, similar teeth were described as possibly belonging to Perleidiformes fish, often assigned to “Colobodus” tooth type (e.g., Diedrich, 2009, 2015; Brachaniec *et al.*, 2015; Nordén *et al.*, 2015).

Wide tooth-plate with dome-shaped teeth in several irregularly arranged and closely spaced rows (Fig. 4H, I). Most of the teeth have flattened apices. Some of them have a delicate, dense striation on the upper part of the crown. In a few cases, rounded, elongated roots are deeply embedded in the tooth plate. In lateral and ventral views, numerous foramina

are present. The tooth-plate belonged to a durophagous fish, probably ‘Colobodus’ (e.g., Diedrich, 2009, 2015; Nordén *et al.*, 2015).

Sauropsida

Sauropsid remains are represented by long bones, vertebrae, teeth, and ribs.

Clade Ichthyopterygia Owen, 1840
Order Ichthyosauria de Blainville, 1835
Family ?Mixosauridae Baur, 1887

Description: A single specimen representing the centrum of an ichthyosaurian vertebra is still embedded in the rock, where it is associated with a well-preserved reptilian rib and bivalves *Plagiostoma* and *Enantiostreon* (Fig. 5A). The centrum is hexagonal in axial view and has a highly concave articulation surface (deeply amphicoelous), having a notochordal character typical of ichthyosaurs (Maisch, 2010). The specimen is slightly taller than wide, indicating a posterior (most probably caudal) position in the skeleton (Fig. 5B, C).

Clade ?Archosauromorpha von Huene, 1946
Order ?Prolacertilla von Huene, 1954
Suborder ?Pretorosauria Huxley, 1871

Description: Small (~4 mm long) and elongated vertebra centrum that is almost twice longer than high and hexagonal in an axial view (Fig. 6A–C). The anterior part of the centrum

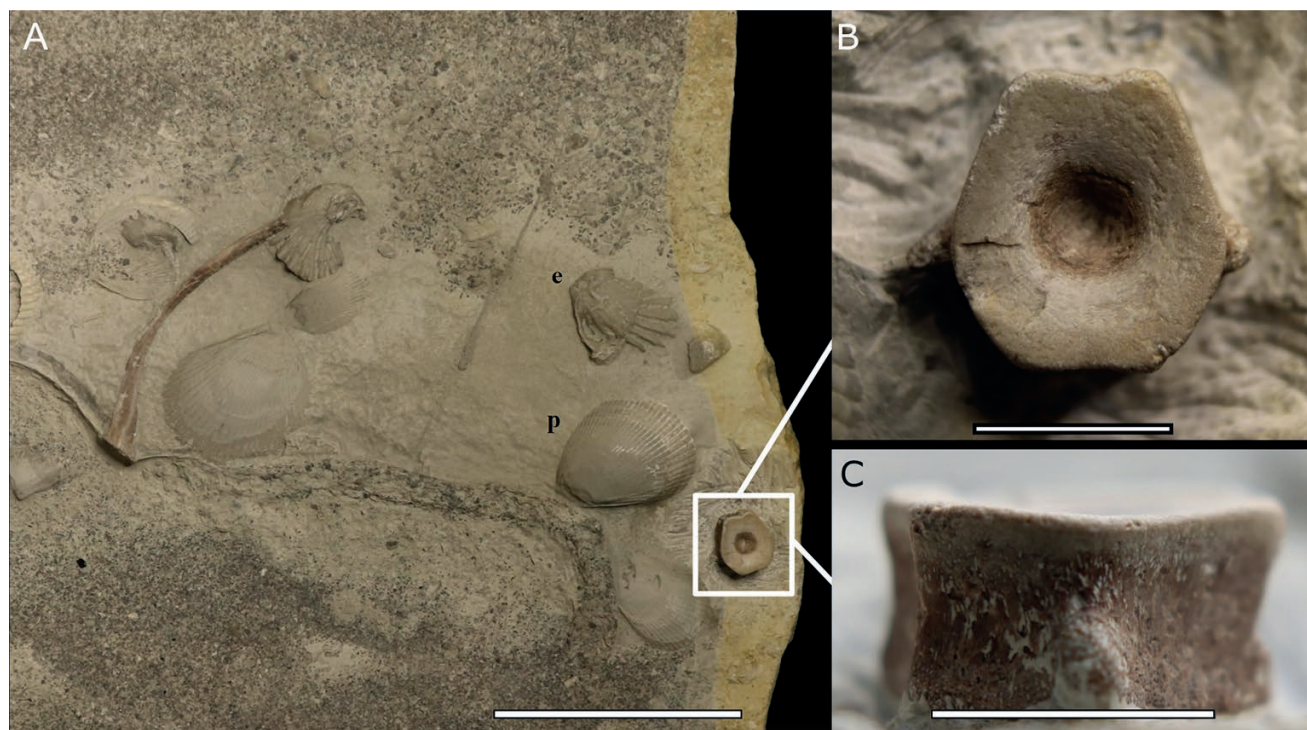


Fig. 5 Ichthyosaur from the Lower Gogolin Beds in Plaza (INGUJ214P/PI/7). **A.** Vertebra centrum associated with reptilian rib (arrow) and shells of bivalve *Plagiostoma* (p) and *Enantiostreon* (e), scale bar: 5 cm. **B, C.** Ichthyosaur vertebra centrum in axial (B) and lateral (C) views, scale bars: 1 cm.

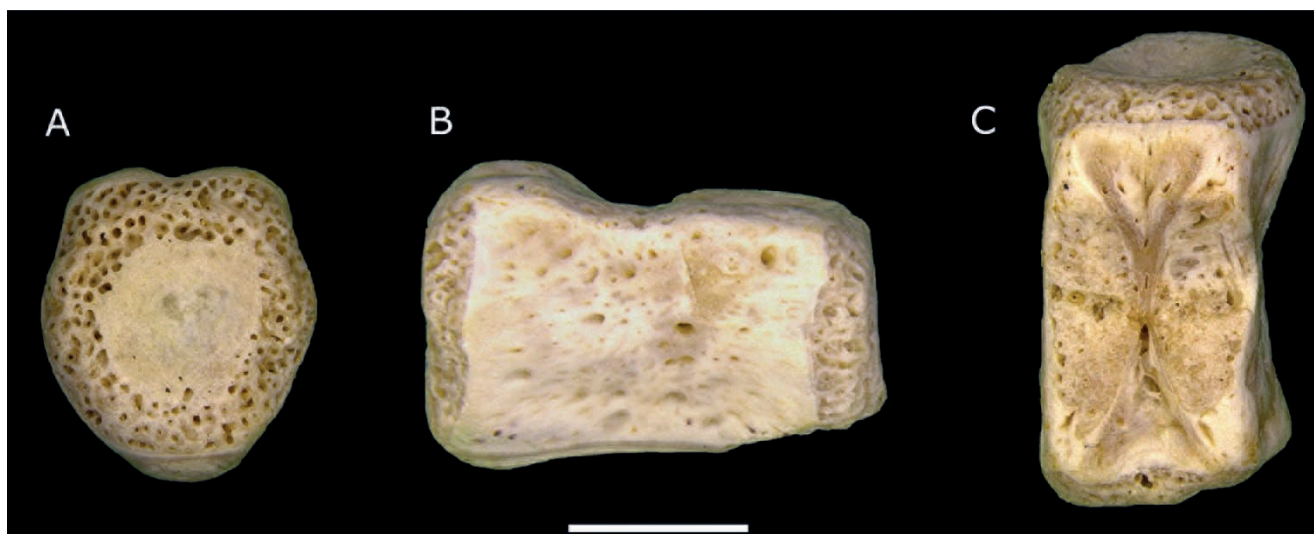


Fig. 6. Reptilian vertebra centrum (with affinities to Proterosauria or basal ichthyosaurids) from Plaza (INGUJ214P/PI/5), in cranial (A), lateral (B), and dorsal (C) views, scale bar: 0.5 mm.

is larger than the posterior one. The anterior articulation surface of the vertebral column is concave; the posterior one is partially destroyed, which hinders the assessment of the original condition. On the dorsal side, the surface, where neural arches were articulated, is still visible. The ventral side of the vertebra possesses a keel, extending over the preserved entire ventral surface of the centrum. The keel is elongated and rectangular in a ventral view. In cranial view it is dorsoventrally flattened and bow-shaped. The whole specimen is poorly ossified and mainly composed of a cancellous bone, which indicates that it belonged to a juvenile individual. Most of the described features can be observed in representatives of proterosaurians such as tanystropheids (e.g., Sennikov, 2011; Oliveira *et al.*, 2018). Nevertheless, the centrum also shows similarities in the shape, size, and morphology of articulation surfaces to basal ichthyosaurids, like *Phalarodon* (Økland *et al.*, 2018).

Clade Eosauropterygia Rieppel, 1994
Family Nothosauridae Baur, 1889

Description: The complete femur was found in the Dąbrowa Górnicza site. The specimen is still embedded within the rock, thus only its ventral and part of the lateral sides are visible. The shaft is straight, slender, and constricted (Fig. 7A), indicating the nothosaurian affinities (Klein *et al.*, 2015).

Ischium is laterally flattened with a maximum length of 16 mm and a width of 14 mm (Fig. 7B). Its dorsal head is substantially expanded, having a fan-like asymmetrical plate. Its anterior part is more medially extended and has a slightly curved, medial margin, whereas the less pronounced, posterior, elongated part has a pronounced, lateral curvature. Both sides of a short shaft are marked by distinct curvatures, with the posterior one being more inclined. The ventral head is around three times narrower than the dorsal one and possesses an almost straight, lateral margin. In the

ventral view, the articulation facet is visible. The specimen belonged to an Eusauropterygian, possibly nothosauroid or to Pistosauroida (cymatosaurid) (Voeten *et al.*, 2014).

Several centra of the thoracic vertebrae of a nothosauroid are slightly longer than wide and oval in axial view. The articulation surfaces indicate an acelous condition. The neural arches are not preserved (Fig. 7C–F).

Nothosaurus tooth crown characterized by a conical shape, strong recurvation, pointed tip, and oval cross-section. It has numerous regularly arranged, longitudinal ridges extending apicobasally (Fig. 7G).

Suborder Pachypleurosauria Nopcsa, 1928
Family ?Pachypleurosauridae Nopcsa, 1928

Description: One obtained vertebra with pachypleurosaurian affinities (similar to those seen in Dactylosaurids from Gogolin; see Bodzioch and Kowal-Linka, 2012) is longer than wide, dorso-ventrally flattened, and elliptical in an axial view. Only one of the articulation surfaces is preserved, which has a concave shape. The neural arch is not preserved, the articulation surface however, is visible. In a ventral view, part of a relatively robust parapophysis (evidence of pachyostosis) and diapophysis are well visible suggesting the pachypleurosaurian affinities (Cheng *et al.*, 2004) (Fig. 7H–K).

Unclassified reptile remains

Many of the isolated specimens are incomplete, very fragmentary, and badly preserved, hindering any detailed description or taxonomic classification. Nevertheless, some of them can be identified as particular skeleton fragments. Long bone fragments are the most abundant, including a probable proximal head of the ulna (Fig. 7O) and distal (Fig. 7P) and proximal heads of the humerus (Fig. 7Q), most probably belonging to a nothosauroid. Ribs (probably nothosaurian) are less common, both complete and

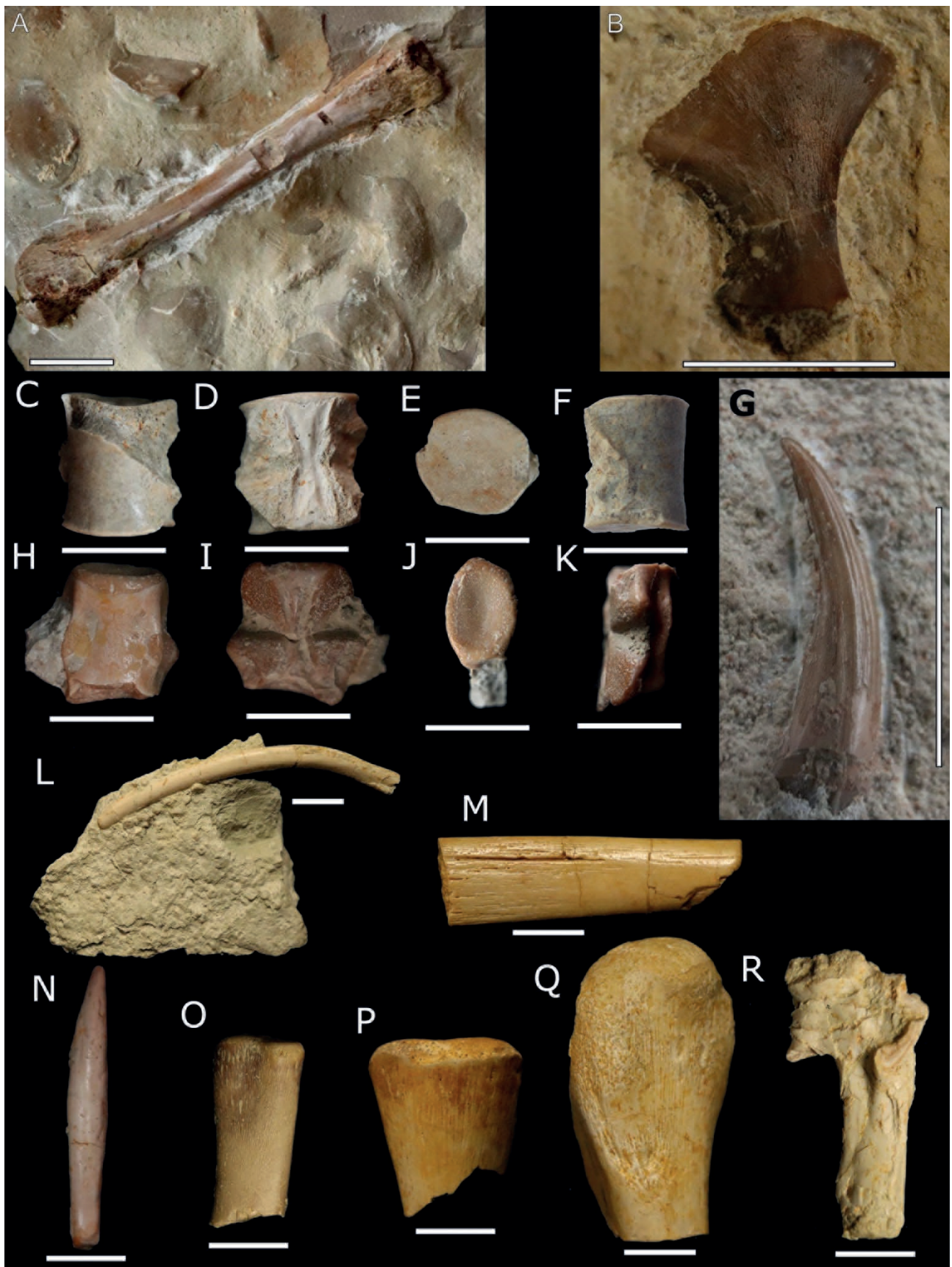


Fig. 7. Reptile remains from the Gogolin Beds in Dąbrowa Górnicza (A, G, INGUJ214P/Zab/0), Żyglin (B, H–R, INGUJ214P/Zy/2–11), and Płaza (C–F). **A.** Nothosauridae femur. **B.** Eusauropterygian ischium. **C–F.** Nothosauridae dorsal vertebra. **G.** Nothosaur tooth. **H–K.** Pachypleurosauria? caudal? vertebra. **L.** Sauropterygian rib. **M.** Fragment of reptilian rib. **N.** Reptilian gastralium. **O.** Probably proximal head of sauropterygian ulna. **P.** Distal head of nothosaurid humerus. **Q.** Proximal head of nothosaurid humerus. **R.** Indeterminate reptilian bone resembling sauropterygian scapula. All scale bars: 1 cm.

incomplete and in different states of preservation. Two of the complete rib specimens (Fig. 7L, M) are quite elongated, highly recurved, and dorso-ventrally flattened. One of them also has a well-preserved head of the rib with articular facets (Fig. 7L).

A single, collected specimen of a reptilian gastralium is short and elliptical in cross-section and terminated with a

pointed end (Fig. 7N). Another incomplete bone fragment may represent the eusauropterygian scapula (Fig. 7R), as implied by the elongated shape of the laterally flattened bone with a rectangular-shaped process, which is however highly damaged, presumably lacking a dorsal part.

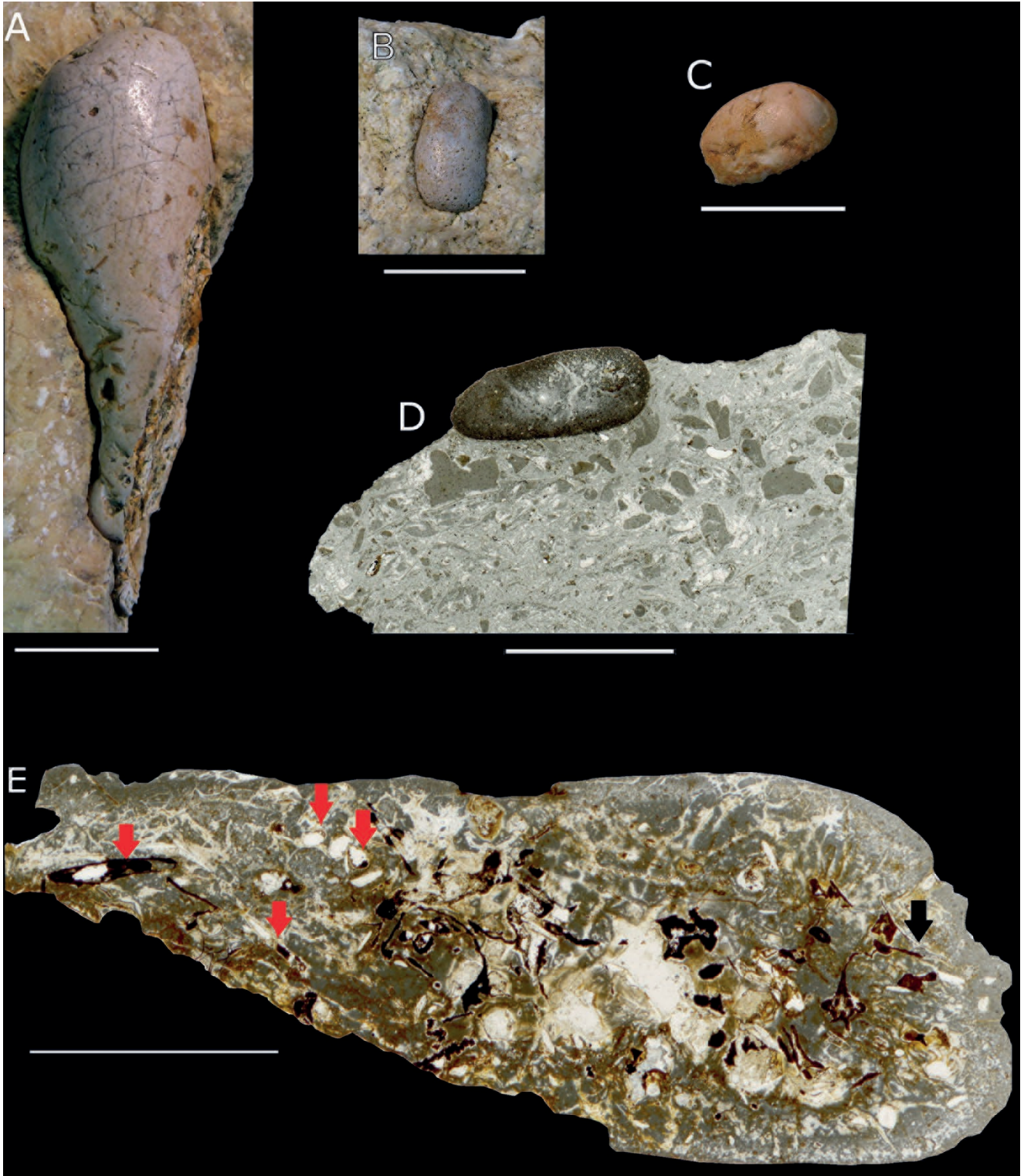


Fig. 8. Coprolites from the Lower Gogolin Beds in Kadzubic. **A–C.** Macroscopic views of coprolites, illustrating three distinct shape types. **D, E.** Thin-section views of coprolite with micritic structure lacking any components (**D**) and with molluscs and worms/serpulids (**E**). Black arrows indicate mollusc shells fragments, red arrows point at worms or serpulids shells. All scale bars: 1 cm.

Coprolites

Vertebrate ichnofossils are represented by coprolites, i.e. fossilized faeces. Coprolites are most commonly found in the fossil record among all products of digestion (bromalites; Hunt, 1992; Northwood, 2005; Salamon *et al.*, 2014; Brachaniec *et al.*, 2015). They often prove to be very informative findings, as not only their content can be identified, but also the putative producers, which may give an insight into prehistoric food webs.

The coprolites collected are pink-grey or yellow-grey and distinct from the host rock and other intraclasts. They are rounded and vary in size from around 1 to 3 cm (Fig. 8). Their surface is smooth and shiny, having a few cracks and lacking any evidence of a spiral structure or striations. Specimen INGUJ214P/Kad/1 is the largest (albeit incomplete), strongly elongated and slightly rectangular (Fig. 8A). Specimen INGUJ214P/Kad/2 is similar in shape, but smaller (about 1 cm; Fig. 8B). Specimen INGUJ214P/Kad/3 is the smallest one and spherical (Fig. 8C).

Observations of two coprolites in thin sections revealed no zonal or spherical structure. Specimen INGUJ214P/Kad/1 is composed of micrite with scattered bivalve fragments, possible worm, or serpulid tubes (Senowbari-Daryan and Link, 2005) and other undetermined bioclasts (Fig. 8E–G). Specimen INGUJ214P/Kad/2 is formed of pure micrite, lacking any components (Fig. 8D).

DISCUSSION AND CONCLUSIONS

Observations of the vertebrate remains from the Muschelkalk deposits of Upper Silesia indicate a distinct diversity in the composition of the vertebrate fauna. The fact that the most fossiliferous beds are the crinoid tempestites highlights storm activity as the main process of transport and accumulation of skeletal material, which was also noted in previous works and at other Muschelkalk sites in Upper Silesia (e.g., Bodzioch, 1985; Chrzastek and Niedzwiedzki, 1998; Szulc, 2007; Surmik, 2010; Kowal-Linka *et al.*, 2014). The fact that the fragments (often abraded) of various animal groups are present in most of the tempestite samples implies intensive mixing of the bone material, originally deposited in different environments: deeper habitats (nektonic carnivore fishes and ichthyosaurs) and nearshore areas (shallow, subtidal durophagous fishes and carnivorous reptiles like nothosaurids). This indicates diversified environments in the time interval discussed and illustrates a strong environmental control on the composition of vertebrate fossil assemblages. Moreover, the differences in abundance and occurrence of different taxa at different sites (Tab. 1) also may imply some geographic differentiation in terms of the accumulation of vertebrate remains. At Mikołów, microfossils of actinopterygians are predominant, but sauropsid fossils are extremely rare and no macrofossils were found during this study. In contrast, chondrichthyans are more abundant at Ząbkowice, whereas reptiles are the most numerous at Żyglin and Płaza, where they are also represented by prolific, isolated macrofossils. However, sampling bias also should be taken into account. Also, differences in fossil abundance can be noted between different beds and

lithologies within the Mikołów profile. Vertebrate microfossils are the most abundant in the thicker tempestite beds. They were also uncovered from the open-platform lime mudstones in the Mikołów profile. However, they usually are less numerous than in the tempestites (with the exception of nodular lime mudstone beds 55 and 56). In the majority of lime mudstones and thin tempestite beds, no vertebrate fossils were found. This observation is evidence for intense storm activity as a main driver of fossil accumulation.

Faunal stratigraphic (temporal) variation throughout the Lower Gogolin Beds in Mikołów was not observed, as the beds studied (both tempestites and lime mudstones) contain comparable fossil associations, composed of similar tooth and scale morphotypes.

The recorded remains represent diverse fish (hybodont sharks: *Acrodus*, cf. *Lissodus* and *Hybodus*, actinopterygians: *Severnichtys*, *Gyrolepis* and durophagous *Colobodus* types of dentition) and sauropsids (mostly eosauropterygians like nothosaurids and probable pachypleurosaurid). Previous studies also recorded *Palaeobates* (Chrzastek, 2008), *Nothosaurus*, *Proneusticosaurus*, *Tanystropheus*, *Dactylosaurus* and a cyamodontoid placodont (Surmik, 2010).

The most noteworthy within this assemblage are the remains of the ichthyosaur, as fossils of this group are generally scarce in the southeastern part of the Germanic Basin (Surmik, 2010). There are only two mentions of ichthyopterygian material from Upper Silesia, concerning the lower jaw of a probable *Mixosaurid* (Surmik, 2010) and more basal *Omphalosaurus* (Wintrich *et al.*, 2017), although there are several more for the entire Germanic Basin (Sander and Mazin, 1993). In contrast to the Polish Middle Triassic fossil record, placodont remains are more abundant in the shallow-marine facies of the central and western parts of the Germanic Basin, especially in the Upper Muschelkalk (e.g., Rieppel, 2000), whereas ichthyosaurs are rare in those areas, although they occur prolifically in the open-marine facies of the north-western Tethys (e.g., Sander, 1989; Maisch and Matzke, 2001; Diedrich, 2012).

Coprolites are common in the Polish part of the Muschelkalk, especially in the Gogolin Beds, and were previously described, e.g., by Salamon *et al.* (2012) and Brachaniec *et al.* (2015). The specimens presented herein are difficult to assign to any specific producers. Their relatively large size, shape, and structure indicate vertebrates as producers (Lucas *et al.*, 2005). Sharks can be excluded, as they produce spiral coprolites (Hunt and Lucas, 2005; Hunt *et al.*, 2007). Coprolites with a relatively large size and numerous bioclasts imply durophagous predation, most probably conducted by colobodontid fishes or sauropterygians.

The specimens presented, along with abundant durophagous fish teeth, may constitute supporting evidence for increased durophagy during the Triassic period, indicated by previous research (e.g., Salamon *et al.*, 2012; Brachaniec *et al.*, 2015). This phenomenon of increased durophagy, together with the appearance of abundant, novel, evolutionary adaptations in benthic invertebrate fauna, associated with the development of defensive strategies, was termed the Mesozoic Marine Revolution (MMR) (Vermeij, 1977). Initially, it was postulated that the MMR started during the Jurassic (Vermeij, 1977). However, subsequent works

demonstrated an earlier commencement of that phenomenon from prolific discoveries of bromalites containing shell material, bite marks on crinoids, and durophagous dentition in the Triassic deposits of Poland (Salamon *et al.*, 2012; Brachaniec *et al.*, 2015) as well as numerous discoveries of predation on crinoids (Baumiller *et al.*, 2010) and a substantial increase in the diversity of marine reptile predators and their morphological variability (Stubbs and Benton, 2016).

On the basis of the fossil and ichnofossil material investigated, it can be concluded that the Silesian vertebrate assemblage at the time of the Early Anisian was already ecologically diverse and represented multilevel, trophic food webs, involving pelagic and nearshore apex predators as well as durophagous feeders. However, the taxa mentioned might have inhabited different and dispersed habitats and their occurrence within some of the layers resulted from re-deposition, due to storm activity.

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