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 notosaurs, pachypleurosaurids, and ichthyosaurs. Also, coprolites of possibly durophagous and predaceous 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 chondrichthians, Żyglin, and Płaza with common sauropsid fossils), sampling bias has to be considered.

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

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; Brachanić 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 (notosaurus, 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
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; Chrząstek and Niedźwiedzki, 1998; Hagdorn and Rieppel, 1999; Chrząstek, 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 (Chrząstek 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 Malopolska 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-ooid-oncoid grainstones-packstones (shoal sands). The sediments overall are strongly...
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Fig. 2. Litostratigraphic 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 Plaża (INGUJ214P/Pl/0).

MATERIAL AND METHODS

The material analysed comprises micro- and macrofossils from Mikołów, Plaża, 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/Pl/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 (sauropterygians 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; Chrząstek and Niedźwiedzki, 1998; Szulc, 2007; Chrząstek, 2008; Kardynał et al., 2016).

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 Chondrichthians, namely hybodontid sharks. The collection consists of placoidal scales, fin spines, and teeth.

**Table 1**

|          | Osteichthyes | Chondrichthyes | Sauropsida |
|----------|--------------|----------------|------------|
|          | *Gyrolepis*  | *Acrodus*      | Nothosauridae |
|          | *Severnichthys* | *Lissodus* | Ichthyosaurus |
|          | *doriphausian* | indet. chondrichthyes | indet. sauropsid |
|          | indet. osteichthyes | | |
| Mikołów | x | x | x |
| Ząbkowice | x | x | |
| Płaza | x | x | x |
| Żyglin | x | | x |

**SYSTEMATIC PALAEONTOLOGY**

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 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).
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.
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 Schultze, 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 teleostomorphs (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 apexes (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

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Fig. 4. Osteichthyes remains from the Lower Gogolin Beds in Ząbkowice (A–G, INGUJ214P/Zab/0), Mikołów (J, INGUJ214P/Mik/55–60) and Plaza (H–I, INGUJ214P/Pl/1–2). A. Macrosemiidae ganoid scale. B. Teleostomorpha ganoid scale. C. Actinopterygiid 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 apexes, 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 apexes. 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 Ichthyoptyeria Owen, 1840**
**Order Ichtyosauria 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...
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 Górnica 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). Nevertheless, the centrum also shows similarities in the shape, size, and morphology of articulation surfaces to basal ichthyosaurids, like *Phalarodon* (Økland et al., 2018).

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 nothosaurid or to Pistosauroidae (cymatosaurid) (Voeten et al., 2014).

Several centra of the thoracic vertebrae of a nothosaurid are slightly longer than wide and oval in axial view. The articulation surfaces indicate an acoelous 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), Żygrlin (B, H–R, INGUJ214P/Zy/2–11), and Plaza (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 gastraliaum 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 Kadłubiec. 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.
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**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 et al., 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; Chrząstek and Niedźwiedzki, 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 (nektic carnivores 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 sauropod fossils are extremely rare and no macrofossils were found during this study. In contrast, chondrichthyan are more abundant at Żyglin and Plazza, 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: *Acrodon*, cf. *Lissodus* and *Hybodus*, actinopterygians: *Severnichthys*, *Gyrolepis* and durophagous *Colobodus* types of dentition) and sauropsids (mostly eosauropterygians like nothosaurids and probable pachypleurosaurid). Previous studies also recorded *Palaeobates* (Chrząstek, 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 ichthopterygian material from Upper Slesia, 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 redeposition, due to storm activity.

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REFERENCES

Agassiz, L., 1837. Recherches sur les Poissons Fossiles. Tome III (livr. 8–9). Imprimerie de Petitpierre, Neuchatel, pp. viii–72.
Agassiz, L., 1838. Recherches sur les Poissons Fossiles. Tome III (livr. 11). Imprimerie de Petitpierre, Neuchatel, pp. 73–140.
Agassiz, L., 1843. Recherches sur les Poissons Fossiles. Tome III (livr. 15–16). Imprimerie de Petitpierre, Neuchatel, pp. 157–390.
Andersson, E., 1916. Über einige Trias-Fische aus der Cava Trefontane, Tessin. Bulletin of the Geological Institutions of the University of Uppsala, 15: 13–33.
Antczak, M. & Bodzioch, A., 2018. Diversity of fish scales in Late Triassic deposits of Krasięjów (SW Poland). Palaeontological Research, 22: 91–100.
Arrambur, C. & Bertin, L., 1958. Super-ordres des holostéens et des halecostomes (Holostei et Halecostomi). Traité de Zoologie: Anatomie, Systématique, Biologie. Angnathes et Poissons: Anatomie, Éthologie, Systématique. Masson et Compagnie, Paris, 13: 2173–2203.
Arratia, G., Scasso, R. & Kiessling, W., 2004. Late Jurassic fishes from Longing Gap, Antarctic Peninsula. Journal of Vertebrate Paleontology, 24: 41–55.
Arratia, G. & Schulze, H. P., 2012. The macrosemiiform fish companion of the Late Jurassic theropod Juraavenator from Schamhaupten, Bavaria, Germany. Fossil Record, 15: 5–25.
Assmann, P., 1933. Die Stratigraphie der oberchelisischen Trias. Teil I: Der Buntsandstein. Jarbuch der Königlich Preußischen Geologischen Landesanstalt, 53: 731–751.
Baumiller, T. K., Salamon, M. A., Gorzelak, P., Mooi, R., Messing, C. G. & Gahn, F. J., 2010. Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. Proceedings of the National Academy of Sciences, 107: 5893–5896.
Berg, L. S., 1937. A classification of fish-like vertebrates. Bulletin de l’Académie des Sciences de l’URSS, 4: 1277–1280.
Baur, G., 1887. Über den Ursprung der Extremitäten der Ichthyopterygia. Berichte über die Versammlungen des Oberrheinischen Geologischen Vereines, 20: 17–20.
Baur, G., 1889. Nothosauridae. In: Zittel, K. A. (ed.), Handbuch der Paläontologie. I. Abth. Paläozoologie. III. Band. Vertebrata (Pisces, Amphibia, Reptilia, Aves). R. Oldenbourg, Munich, 478 pp.
Benton, M. J., Zhang, Q., Hu, S., Chen, Z.-Q. & Wen, W., 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. Earth-Science Reviews, 125: 199–243.
Blainville, H. M. D., 1835. Description de quelques espèces de la Californie, précédée de l’analyse d’un système général d’érpetologie et d’amphibiologie. Nouvelles Archives de Muséum d’Histoire Naturelle, 4: 236–296.
Bodzioch, A., 1985. Palaeoecology and sedimentary environment of the Terebratula Beds (Lower Muschelkalk) from Upper Silesia (South Poland). Annales Societatis Geologorum Poloniae, 55: 127–138.
Bodzioch, A. & Kowal-Linka., M., 2012. New finds of vertebrate remains from the Röt (Lower Triassic, Olenkian) in the vicinity of Gogolin (Opole Silesia, southern Poland). In: Jagt-Yazykova, E., Jagt, J. W. M., Bodzioch, A. & Konietzko-Meier, D. (eds), Krasięjów – Palaeontological Inspiration. ZPW “Plik”, Bytom, pp. 70–80.
Bonaparte, C. L. J. L., 1838. Selachium tabula analytica. Nuovi Annali delle Scienze Naturali, 1: 195–214.
Botfalvai, G., Gyori, O., Pozsgai, E., Farkas, I. M., Sági, T., Szabo, M. & Ősi, A., 2019. Sedimentological characteristics and palaeoenvironmental implication of Triassic vertebrate localities in Villány (Villány Hills, Southern Hungary). Geologica Carpathica, 70: 135–152.
Böttcher, R., 2015. Fische des Lettenkeupers. In: Hagdorn, H., Schoch, R. & Schweigert, G. (eds), Der Lettenkeuper – Ein Fenster in die Zeit vor den Dinosauriern. Staatliches Museum für Naturkunde, Stuttgart, Ingelfingen, pp. 141–202.
Brachaniec, T., Niedźwiedzki, R., Surmik, D., Krzykawski, T., Szopa, K., Gorzelak, P. & Salamon, M. A., 2015. Coprolites of marine vertebrate predators from the Lower Triassic of southern Poland. Palaeogeography, Palaeoclimatology, Palaeoecology, 435: 118–126.
Brough, J., 1935. On the structure and relationships of the hybodont sharks. Memoirs and Proceedings of the Manchester Literary and Philosophical Society, 79: 35–50.
Casier, E., 1959. Contributions a l’étude des poissons fossiles de la Belgique XII. Sélaciens et Holocéphales sinémuriens de la province de Luxembourg. Institut Royal des Sciences Naturelles de Belgique Bulletin, 35: 1–27.
Cavicchini, J., Heyworth, H. C., Duffin, C. J., Hildebrandt, C. & Benton, M., 2018. A Rhaetian microvertebrate fauna from Stowey Quarry, Somerset, U.K. Proceedings of the Geologists’ Association, 129: 144–158.
Chen, Z.-Q. & Benton, M., 2012. The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nature Geoscience*, 5: 375–383.

Cheng, Y., Wu, X. & Ji, Q., 2004. Triassic marine reptiles give birth to live young. *Nature*, 432: 383–386.

Chrzastek, A., 2008. Vertebrate remains from the Lower Muschelkalk of Raciborowice Górze (North-Sudetic Basin, SW Poland). *Geological Quarterly*, 52: 225–238.

Chrzastek, A. & Niedźwiedzki, R., 1998. Vertebrates of the Roetian and Lower Muschelkalk in Silesia. *Prace Geologiczno-Mineralogiczne*, 54: 69–81. [In Polish, with English summary.]

Cope, E. D., 1872. *Observations on the systematic relations of the fishes. Proceedings of the American Society for the Advancement of Science*, 20: 317–343.

DeMar, D. G. Jr., 2012. *An Illustrated Guide to Latest Cretaceous Vertebrate Microfossils of the Hell Creek Formation of Northeastern Montana*. http://digfieldschool.org/wp-content/uploads/2013/08/Fossil-ID-Guide_06_28_12.pdf [26–11–2018].

Diedrich, C. G., 2015. The vertebrates from the Lower Ladinian (Middle Triassic) bonebed of Lamerden (Germany) as palaeoenvironment indicators in the Germanic Basin. *Open Geosciences*, 7: 1–28.

Diedrich, C., 2009. The vertebrates of the Anisan/Ladinian boundary (Middle Triassic) from Bissendorf (NW Germany) and their contribution to the anatomy, palaeoecology, and palaeobiogeography of the Germanic Basin reptiles. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 273: 1–16.

Diedrich, C., 2012. The Middle Triassic marine reptile biodiversity in the Germanic Basin, in the centre of the Pangaean world. *Central European Journal of Geosciences*, 4: 9–46.

Duffin, C. J., 1999. Stop 14. Fish. In: Swift, A. & Martill, D. M. (eds), *Fossil of the Rhaetian Peneath Group*. The Palaeontological Association, London, pp. 191–222.

Eck, H., 1865. *Über die Formationen des bunten Sandsteins und des Muschelkalks in Oberschlesien und ihre Versteinerungen*. R. Friedländer und Sohn, Berlin, 149 pp.

Giordano, P. G., Arratia, G. & Schultze, H. P., 2016. Scale morphology and specialized dorsal scales of a new teleosteomorph fish from the Aptian of West Gondwana. *Fossil Record*, 19: 61–81.

Hagdorn, H. & Rieppel, O., 1999. Stratigraphy of marine reptiles in the Triassic of Central Europe. *Zentralblatt für Geologie und Paläontologie*, 7–8: 651–678.

Hay, O. P., 1902. Bibliography and catalogue of the fossil vertebrates of North America. *Bulletin of the United States Geological Survey*, 179: 1–868.

Herman, J., 1977. Les Sélaciens des terrains néoércétiques & paléocènes de Belgique & des contrées limitrophes. Éléments d’une biostratigraphie intercontinentale. Mémoires pour servir à l’explication des Cartes géologiques et minières de la Belgique, 15: 1–450.

Huene, F., von, 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologisches Zentralblatt*, 65: 268–275.

Huene, F., von, 1954. *Die Sauierwelt und ihre Geschichtlichen Zusammenhänge*. Gustav Fischer Verlag, Jena, 66 pp.

Hunt, A. P., 1992. Late Pennsylvanian coprolites from the Kinney Brick Quarry, central New Mexico, with notes on the classification and utility of coprolites. *New Mexico Bureau of Mines and Mineral Resources Bulletin*, 138: 221–229.

Hunt, A. P. & Lucas, S. G., 2005. A new coprolite ichnotaxon from the Early Permian of Texas. In: Lucas, S. G. & Zeigler, K. E. (eds), *The nonmarine Permian*. New Mexico Museum of Natural History and Science Bulletin, 30: 121–122.

Hunt, A. P., Lucas, S. G., Spielmann, J. A. & Lerner, A. J., 2007. A review of the vertebrate coprolites of the Triassic with descriptions of new Mesozoic ichnotaxa. In: Lucas, S. G. & Spielmann, J. A. (eds), *The Global Triassic*. New Mexico Museum of Natural History and Science Bulletin, 41: 88–98.

Huxley, T. H., 1871. *A Manual of the Anatomy of Vertebrated Animals*. J. & A. Churchill, London, 510 pp.

Huxley, T. H., 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society*, 43: 649–662.

Jiang, D., Motani, R., Hao, W., Rieppel, O., Sun, Y., Tintori, A., Sun, Z. & Schmitz, L., 2009. Biodiversity and sequence of the Middle Triassic Panxian marine reptile fauna, Guizhou Province, China. *Acta Geologica Sinica – English Edition*, 83: 465–470.

Kardynal, K., Kowalski, J., Bodzioch, A. & Kowal-Linka, M., 2016. Remains of small vertebrates from the Röt (Lower Triassic) of Gogolin (Opole region, Poland). In: Holwerda, F., Madern, A., Voeten, D., van Heteren, A., Liston, J., Meijer, H. & den Ouden, N. (eds), *XIV EAVP Meeting, 6–10 July, 2016*. Koninklijke Nederlandse, Akademie van Wetenschappen, Haarlem, The Netherlands, p. 186.

Klein, N., Voeten, D.F.A.E., Lankamp, J., Bleeker, R., Sichelschmidt, O. J., Liebrand, M., Nieweg, D. C. & Sander, P. M., 2015. Postcranial material of *Nothosaurus marichius* from the Lower Muschelkalk (Anisan) of Winterswijk, The Netherlands, with remarks on swimming styles and taphonomy. *Palaeontologische Zeitschrift*, 89: 961–981.

Kowal-Linka, M., Jochum, K. P. & Surnik, D., 2014. *LA-ICP-MS analysis of rare earth elements in marine reptile bones from the Middle Triassic bonebed (Upper Silesia, S Poland): impact of long-lasting diagenesis, and factors controlling the uptake*. *Chemical Geology*, 363: 213–228.

Landon, E. N. U., Duffin, C. J., Hildebrandt, C., Davies, T. G., Simms, M. J. & Benton, M. J., 2017. The discovery of crinoids and cephalopod hooklets in the British Triassic. *Proceedings of the Geologists Association*, 128: 360–373.

Langenhan, A., 1911. *Versteinerungen der deutschen Trias (des Buntsandsteins, Muschelkalks und Keupers) auf Grund eigener Erfahrungen zusammengestellt und auf Stein gezeichnet*. Selbstverlag, Friedrichsroda, 10 pp.

Liszkowski, J., 1993. Die Selachierfauna des Muschelkalks in Polen: Zusammensetzung, Stratigraphie und Paläoökologie. In: Hagdorn, H. & Seilacher, A. (eds), *Muschelkalk. Schöntaler Symposium*. Goldschnack, Korb, pp. 177–185.

Lucas, S. G., Harris, S. K., Spielmann, J. A., Berman, D. S., Henrici, A. C., Heckert, A. B., Zeigler, K. E. & Rinehart, L. F., 2005. Early Permian vertebrate biostratigraphy at Arroyo del Agua, Rio Arriba County, New Mexico. In: Lucas, S. G., Zeigler, K. E. & Spielmann, J. A. (eds), *The Permian of Central New Mexico*. New Mexico Museum of Natural History and Science Bulletin, 31: 163–169.
Maisch, M. W., 2010. Phylogeny, systematics, and origin of the Ichthyosauria – the state of the art. *Palaeodiversity*, 3: 151–214.

Maisch, M. W. & Matzke, A. T., 2001. Observations on Triassic ichthyosaurs. Part VIII. A redesription of *Phalarodon major* (von Huene, 1916) and the composition and phylogeny of the Mixosauridae. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 220: 431–447.

Märss, T., 2006. Exoskeletal ultrasculpture of early vertebrates. *Journal of Vertebrate Paleontology*, 26: 235–252.

Matysik, M., 2014. Sedimentology of the “ore-bearing dolomite” of the Kraków-Silesia region (Middle Triassic, southern Poland). *Annales Societatis Geologorum Polonae*, 84: 81–112.

Matysik, M., 2016. Facies types and depositional environments of a morphologically diverse carbonate platform: A case study from the Muschelkalk (Middle Triassic) of Upper Silesia, Southern Poland. *Annales Societatis Geologorum Polonae*, 86: 119–164.

Matysik, M., 2019. High-frequency depositional cycles in the Muschelkalk (Middle Triassic) of southern Poland: Origin and implications for Germanic Basin astrochronological scales. *Sedimentary Geology*, 383: 159–180.

Matysik, M. & Surmik, D., 2016. Depositional conditions of vertebrate remains within the Lower Muschelkalk (Anisian) peritidal carbonates of the “Stare Gliny” quarry near Olkusz (Kraków-Silesia region, southern Poland). *Przegląd Geologiczny*, 64: 495–503. [In Polish, with English summary.]

Meyer, H. von, 1849. Fische, Crustaceen, Echinodermen und andere Versteinerungen aus dem Muschelkalk Oberschlesiens. *Palaeontographica*, 1: 243–279.

Nopcsa, F., 1928. The genera of reptiles. *Palaeobiologica*, 1: 163–188.

Nordén, K. K., Duffin, C. J. & Benton, M. J., 2015. A marine vertebrate fauna from the Late Triassic of Somerset, and a review of British placodonts. *Proceedings of the Geologists Association*, 126: 564–581.

Northwood, C., 2005. Early Triassic coprolites from Australia and their palaeobiological significance. *Palaeontology*, 48: 49–68.

Ołkand, I. H., Delsett, L. L., Roberts, A. J. & Hurum, J. H., 2018. A *Phalarodon fraasi* (Ichthyosauria: Mixosauridae) from the Middle Triassic of Svalbard. *Norwegian Journal of Geology*, 98: 267–288.

Oliveira, T. M., Oliveira, D., Schultz, C. L., Kerber, L. & Pinheiro, F. L., 2018. Tanystrophen archosauromorphs in the Lower Triassic of Gondwana. *Acta Palaeontologica Polonica*, 63: 713–723.

Owen, R., 1840. Report on British fossil reptiles. *Report of the British Association for the Advancement of Science*, 9: 43–126.

Patterson, R. T., Wright, C., Chang, A. S., Taylor, L. A., Lyons, P. D., Dallimore, A. & Kumar, A., 2002. Atlas of common squamatological (fish scale) material in coastal British Columbia and an assessment of the utility of various scale types in paleofisheries reconstruction. *Palaeontologica Electronica*, 4: 1–88.

Regan, C. T., 1923. The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. *Proceeding of the Zoological Society of London*, 1923: 445–461.

Rieppel, O., 1994. Osteology of Simosaurus gaillardoti and the relationships of stem-group Sauropterygia. *Fieldiana: Geology*, 28: 1–85.

Rieppel, O., 2000. Sauropterygia I – Placodontia, Pachypleurosauria, Nothosauroida, Pistosauroida. In: Wellhofer, P. (ed.), *Encyclopedia of Paleoherpotology*. Verlag Dr. Friedrich Pfeil, Munich, 134 pp.

Rieppel, O. & Hagdorn, H., 1998. Fossil reptiles from the Spanish Muschelkalk (Mont-Ral and Alcover, Province Tarragona). *Historical Biology*, 13: 77–97.

Roemer, F., 1870. *Geologie von Oberschlesien*. Robert Nischkowsky, Breslau, 587 pp.

Salamon, M. A., Gorzelak, P., Niedźwiedzki, R., Trzęsiok, D. & Baumiller, T. K., 2014. Trends in shell fragmentation as evidenced of mid-Paleozoic changes in marine predation. *Paleobiology*, 40, 14–23.

Salamon, M. A., Niedźwiedzki, R., Gorzelak, P., Lach, R. & Surmik, D., 2012. Bromalites from the Middle Triassic of Poland and the rise of the Mesozoic Marine Revolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 321–322: 142–150.

Sander, P. M., 1989. The large ichthyosaur *Cymbospondylus buchseri* sp. nov., from the Middle Triassic of Monte San Giorgio (Switzerland), with a survey of the genus in Europe. *Journal of Vertebrate Paleontology*, 9: 163–173.

Sander, P. M. & Mazin, J. M., 1993. The paleobiogeography of Middle Triassic ichthyosaurs: The five major faunas. *Paleontologia Lombarda*, 2: 145–152.

Scheyer, T. M., Romano, C., Jenks, J. & Bucher, H., 2014. Early Triassic marine biotic recovery: the predators’ perspective. *PLoS ONE*, 9: e88987.

Schmidt, M., 1928. *Die Lebewelt unserer Trias*. Rau, Öhringen, 461 pp.

Schmidt, M., 1938. *Die Lebewelt unserer Trias*. Rau, Öhringen, 144 pp.

Sennikov, A. G., 2011. New tanystrophoids (Reptilia: Archosauriomorphia) from the Triassic of Europe. *Paleontological Journal*, 45: 90–104.

Senowbari-Daryan, B. & Link, M., 2005. *Filograna* (colonial serpulid worm tubes) from Upper Triassic (Norian) reef boulders of Taurus Mts. (southern Turkey). *Facies*, 51: 454–459.

Sibert, E. C., Cramer, K. L., Hastings, P. A. & Norris, R. D., 2017. Methods for isolation and quantification of microfossil fish teeth and elasmobranch dermal denticles (ichthyoliths) from marine sediments. *Palaeoecology Electronica*, 20.1.2T: 1–14.

Slater, T. S., Duffin, C. J., Hildebrandt, C., Davies, T. G. & Benton, M. J., 2016. Microvertebrates from multiple bone beds in the Rhaetian of the M4–M5 motorway junction, South Gloucestershire, U.K. *Proceedings of the Geologists’ Association*, 127: 464–477.

Stachacz, M. & Matysik, M., 2020. Early Middle Triassic (Anisian) trace fossils, ichnofabrics, and substrate types from the southeastern Germanic Basin (Wellenkalk facies) of Upper Siliesia, southern Poland: Implications for biotic recovery following the Permian/Triassic mass extinction. *Global and Planetary Change*, 194, 103290, https://doi.org/10.1016/j.gloplacha.2020.103290.
DIVERSITY OF VERTEBRATE REMAINS

Stockar, R., 2010. Facies, depositional environment, and palaeoecology of the Middle Triassic Cassina beds (Meride Limestone, Monte San Giorgio, Switzerland). *Swiss Journal of Geosciences*, 103: 101–119.

Storrs, G. W., 1994. Fossil vertebrate faunas of the British Rhaetian (latest Triassic). *Zoological Journal of the Linnean Society*, 112: 217–259.

Stubbs, T. L. & Benton, M. J., 2016. Ecomorphological diversifications of Mesozoic marine reptiles: the roles of ecological opportunity and extinction. *Palaeobiology*, 42: 547–573.

Surmik, D. & Brachaniec, T., 2013. The large superpredators’ teeth from Middle Triassic of Poland. *Contemporary Trends in Geoscience*, 2: 91–94.

Surmik, D., 2010. Preliminary taphonomical analysis of Lower Muschelkalk bone accumulation in Silesia (Poland). In: Nowakowski, D. (ed.), *Morphology and Systematic of Fossil Vertebrates*. DN Publisher, Wrocław, pp. 110–117.

Szulc, J., 2000. Middle Triassic evolution of the northern Peri-Tethys area as influenced by early opening of the Tethys Ocean. *Annales Societatis Geologorum Poloniae*, 70: 1–48.

Szulc, J., 2007. Stop II. 4. Stare Gliny: active quarry. In: Szulc, J., Becker, A. (eds), *International Workshop on the Triassic of Southern Poland: Pan-European Correlation of the Epicontinental Triassic, 4th Meeting, September 3–8, 2007. Fieldtrip Guide*. Polish Geological Society, Polish Geological Institute, Institute of Geological Sciences, Jagiellonian University, Cracow, pp. 60–61.

Śliwiński, S., 1964. The geology of the Siewierz area (Upper Silesia). *Prace Geologiczne Polskiej Akademii Nauk, Oddział w Krakowie*, 25: 1–74. [In Polish, with English summary.]

Thollière, V., 1858. Note sur les poissons fossiles du Bugey, et sur l’application de la méthode de Cuvier à leur classement. *Bulletin de la Société géologique de France*, 15: 782–793.

Vermeij, G. J., 1977. The Mesozoic Marine Revolution: Evidence from snails, predators and grazers. *Paleobiology*, 3: 245–258.

Voeten, D. F. A. E., Sander, P. M. & Klein, N., 2014. Skeletal material from larger Eusauropterygia (Reptilia: Eosauropterygia) with nothosaurian and cymatosaurian affinities from the Lower Muschelkalk of Winterswijk, the Netherlands. *Paläontologische Zeitschrift*, 89: 943–960.

Wintrich, T., Jagdorn, H. & Sander, P. M., 2017. An enigmatic marine reptile-the actual first record of *Omphalosaurus* in the Muschelkalk of Germanic Basin. *Journal of Vertebrate Paleontology*, e1384739.

Zangerl, R., 1981. *Chondrichthyes I: Paleozoic Elasmobranchii. Handbook of Paleichthyology, Volume 3a*. Dr. Friedrich Pfeil, München, 113 pp.