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ARTICLE

A NEW MIDDLE TRIASSIC VERTEBRATE ASSEMBLAGE FROM MIEDARY (SOUTHERN POLAND)

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ABSTRACT—The Middle Triassic remains a poorly understood time in the evolution of land vertebrates. Here, we report a new Ladinian-age vertebrate assemblage from Miedary (southern Poland). It consists of more than 20 taxa including fish (four species of Hybodontiformes, cf. *Gyrolepis*, Redfieldiiformes, '*Thelodus*', *Saurichthys*, *Serrolepis*, *Prohalecites*, *Ptychoceratodus*), amphibians (*Mastodonsaurus*, *Gerrothorax*, *Plagiosternum*, chroniosuchian *Bystrowiella*), and reptiles (Owenettidae, *Blezingeria*, *Nothosaurus*, *Tanystropheus*, an additional, yet unidentified tanystropheid, the doswelliid *Jaxtasuchus*, and another archosauromorph, as well as eight archosauriform tooth morphotypes). Preliminary comparisons suggest biogeographic and environmental similarities with roughly contemporaneous localities known from the southwestern part of the Germanic Basin. Among differences in these two areas are the presence of a new armored archosauromorph and a surprising abundance of *Tanystropheus* remains in the new Polish site. Miedary is currently the richest source of three-dimensionally preserved *Tanystropheus* material in the world, which will be crucial for a better understanding of the preferred environment and lifestyle of this highly specialized reptile.

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INTRODUCTION

The fossil record of the Triassic continental ecosystems is very unevenly recognized in terms of geography and stratigraphy (Dunhill & Wills, 2015). For instance, numerous Upper Triassic vertebrate localities contrast in their quantity with much less abundant Middle Triassic sites (Sues & Fraser, 2010). This difference is becoming even more pronounced because of recent developments in absolute dating of Triassic rocks. Sediments long considered as Middle Triassic, such as the Chānares Formation in Argentina, Lifua Member of the Manda Beds in Tanzania, or *Dinodontosaurus* Assemblage Zone in Brazil, are possibly much younger, Upper Triassic or close to the Middle/Upper Triassic boundary (Marsicano et al., 2016; Martinelli et al., 2017; Ottone et al., 2014; Wynd et al., 2017). These developments result in a significant stratigraphic gap in the fossil record of numerous continental vertebrate groups, in particular stem mammals, lissamphibians, archosaurs, stem turtles, lepidosauromorphs, and freshwater neopterygians, which developed crucial anatomical adaptations in the Triassic (Arratia, 2015; Dalla Vecchia, 2013; Evans & Borsuk-Białynicka, 1998; Li et al., 2008; Pardo et al., 2017; Piechowski & Tałanda, 2020; Schoch et al., 2020; Sobral et al., 2020; Soul & Benson, 2017; Sterli et al., 2021; Sulej et al., 2020; Szczygielski & Słowiak, 2022; Szczygielski & Sulej, 2019; Whiteside, 1986). Later in the Mesozoic and Cenozoic, these groups dominated the terrestrial and aquatic ecosystems, but in the Triassic they coexisted with numerous other vertebrates (e.g., dicynodonts, rhynchosaurs, tanystropheids, chroniosuchians, doswellids, procolophonians, placodonts, capitosaurian temnospondyls, perleidiforms) that probably did not survive into the Jurassic (Dunhill & Wills, 2015).

Numerous outcrops of the Lower Keuper deposits in southern Germany provided abundant late Ladinian assemblages of mixed-marine, freshwater, and terrestrial vertebrates (Damiani et al., 2009; Gower & Schoch, 2009; Hagdorn et al., 2015; Jones et al., 2013; Mujal et al., 2022; Schoch, 1997, 2000, 2008, 2011; Schoch & Seegis, 2016; Schoch & Sues, 2014, 2015, 2018; Schoch et al., 2018, 2022; Sobral et al., 2020, 2021; Sues & Schoch, 2013; Sues et al., 2020, 2022; Wild, 1980; Witzmann et al., 2008, 2012). Their stratigraphic position is securely correlated with marine biostratigraphy due to their lateral association with fully marine facies within the Germanic Basin (Franz et al., 2013). That is why outcrops of the Lower Keuper are of great importance for the global vertebrate record.

Here, we investigate a new, probably early Ladinian (see Pawlak et al., 2022), vertebrate assemblage from Miedary (southern Poland) that is also situated within the Germanic Basin but hundreds of kilometers away from the other major Lower Keuper sites. The locality was briefly described by Sulej

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et al. (2011) who found palynomorphs confirming the Ladinian age of the site, traces of various invertebrates, the bivalve *Costatoria goldfussi*, shark teeth and ganoid scales, as well as teeth and bones of nothosaurids and archosaurs (Sulej et al., 2011). However, the previous study was restricted to the uppermost beds (carbonates and grayish claystones), which were the only ones exposed at that time. Our team revisited the locality in 2014 and discovered a new fossiliferous layer near the bottom of the claypit, dominated by clastic rocks. Pawlak et al. (2022) described vertebrate microfossil assemblages from this new bed and from the carbonates, both dominated by fish remains with accessory contribution of tetrapod teeth. Here, we provide a description of the most diagnostic vertebrate macrofossils from this recently discovered layer, allowing for a preliminary assessment of their taxonomic diversity. We discuss its biogeographic context and peculiar vertebrate assemblage.

GEOLOGICAL SETTING

The Germanic Basin was an extensive depression reaching from modern eastern England to eastern Poland. In the Middle Triassic, it was occupied by a shallow sea, which deposited the thick, carbonate-dominated succession of the Muschelkalk facies. The Muschelkalk Sea was a relatively restricted reservoir, connected with the nearby Tethys via three gates. From the paleontological perspective, the Muschelkalk fauna is diverse but generally represents a depleted set of taxa known from the Tethys (Szulc, 2000). The Ladinian was a time of long-lasting marine regression from the Germanic Basin. It produced a lithologically variable, clastic-carbonate series composed of interbedding shallow-marine, marginally marine and fluvial deposits called the Lower Keuper (Franz et al., 2013). The more continental conditions of the Lower Keuper deposition are reflected also by the fauna, which deviates from the one known from the Tethys, due to the spread of taxa related with less saline and freshwater settings in the remnants of the Muschelkalk Sea.

The Lower Keuper in the Upper Silesia region is poorly studied despite a long history of research. Contrary to the classic outcrops in south-western Germany, no cyclicity nor traceable marker horizons have been recognized yet. The earliest notes about existence of the Lower Keuper deposits in Upper Silesia region were provided by Eck (1863), Roemer (1870), and Assmann (1913a, b, 1914). They recognized outcrops of this unit in the vicinities of the Rozmierka and Miedary villages, on which the earliest descriptions of the occurring lithologies were based. The reported lithologies comprised grayish claystones interbedded by brownish dolostones and reddish to greenish clastics. Further studies on the Upper Silesian Triassic lithostratigraphy informally referred to such deposits as the Miedary Beds (Fig. 1B; see Kotlicki, 1974, 1995).

While numerous vertebrate fossils were reported from the Ladinian outcrops in the vicinity of Miedary by Meyer (1847, 1847–1855, 1849), Eck (1862, 1865), Gürich (1884), Langenhan (1903) Assmann (1913a, 1914), and possibly Huene (1916), we do not find evidence of any of these works referring to the currently discussed locality. Most of the aforementioned authors described elements of the fauna from the "Rybnaer Kalk," as originally called by them, which consisted of marine fishes—numerous hybodontiforms, *Colobodus*, *Gyrolepis*, *Saurichthys*, and tetrapods—nothosaurids, pistosaurids, placodonts, as well as some singular finds of *Tanystropheus* and a putative ichthyosaur. According to the current stratigraphic subdivision, this fauna should be considered as coming from the Upper Muschelkalk (possibly Boruszowice Beds). Assman (1913a) was the first to assign an assemblage of ichthyoliths (hybodonts and actinopterygians) unearthed near Miedary to the Lower Keuper. However, according to the cartographic documentation (Assmann, 1913b), this fossil assemblage came from an outcrop exposing the uppermost Muschelkalk section, located closer to the Laryszów village than to the current site. Recently it was suggested that some of the historical specimens originated from the Miedary claypit (Skawiński et al., 2017), but the local brickyard started excavations therein in the 1910s at earliest (see Assmann, 1913b), while the mentioned specimens were collected in the 1840s at latest. Somewhere in the second half of the 20th century, vertebrate fossils indistinguishable from those originating from the outcrop described herein were collected by A. Tokarski. They were not published and remain in the collection of the Polish Geological Institute (Warsaw, Poland). Hence, there is no evidence that any fossils from the new Miedary locality were described before the publications of Sulej et al. (2011) and Pawlak et al. (2022) and thus the site should be treated as novel.

The vertebrate-bearing site described herein is located between Miedary and Laryszów villages, about 1 km to the west from the historical outcrop in Laryszów. The exposed section is 5 m thick, and comprises three distinct units: the lower unit composed of clastic rocks ("Unit 1" in Fig. 1C), the middle unit composed of claystones and mudstones ("Unit 2" in Fig. 1C), and the upper unit composed of carbonates with insertions of clastic material. The fossils described herein come from two distinct packages: the glauconite beds (M1–M2) and argillaceous mudstone (M3), both located in the lowermost part of the section.

The glauconite beds have a complicated internal structure. The succession starts with a variegated, reddish to yellowish sandstone, strongly lithified by a carbonate cement (M1). The glauconite is scattered in sediment and forms patchy, irregular concentrations. No lamination is visible. A notable feature of this layer are numerous root traces up to two centimeters in diameter. The vertebrate bones are very common here and usually form multitaxic clusters of disarticulated elements with apparently random content. Bones in the clusters are often adjacent to each other. The thickness of this layer is unknown, as it reaches the bottom of the claypit, although it measures at least 20 cm. The upper limit of the M1 layer is sharp. It is followed by a continuous layer of green sandstone rich in glauconite, which is evenly abundant within the entire bed (M2a). The disarticulated shell accumulations occur commonly in this layer. Similarly to the underlying package, vertebrate bones are abundant herein and form clusters, but are frequently found as isolated specimens as well. Fish microfossils are also abundant. The M2a layer is about 15 cm thick on average, although locally its thickness drops to only 2–5 cm. It smoothly passes into the M2b layer composed of alternating greenish and reddish facies. In this layer glauconite is concentrated in green, horizontal, tempestite-like interbeds. They are lithologically similar to the M2a layer but some of them are especially enriched in mica flakes and fish microfossils. The distribution of larger bones is similar to the M2a layer but isolated bones are more common. The interbeds are often hummocky cross-stratified, whereas others tend to not exhibit any lamination. The thickness of the interbeds varies, reaching up to 10 cm, but usually does not exceed 5 cm. They intercalate in a reddish mudstone with various glauconite content. The bulk of the latter, if present, is concentrated in irregular, patchy concentrations. The mudstone has a poorly accented horizontal lamination. Vertebrate fossils in the reddish facies are less common, yet tend to show higher degree of articulation than in the underlying or interbedding glauconite-rich sandstones. Most of the bone associations representing remains of single individuals come from the reddish facies. The M2b layer is about 40 cm thick. It ends with a sharp erosional boundary and abrupt change of lithology.

The sediment directly overlying the glauconite beds is devoid of observable glauconite grains and shows a higher clay content (M3). The thickness of this bed is variable, ranging from 5 up to 20 cm. It is rich in numerous vertical, gray-colored dykes of unknown origin, which partially penetrate the underlying layers too. Thin, horizontal zones of grayish sediment

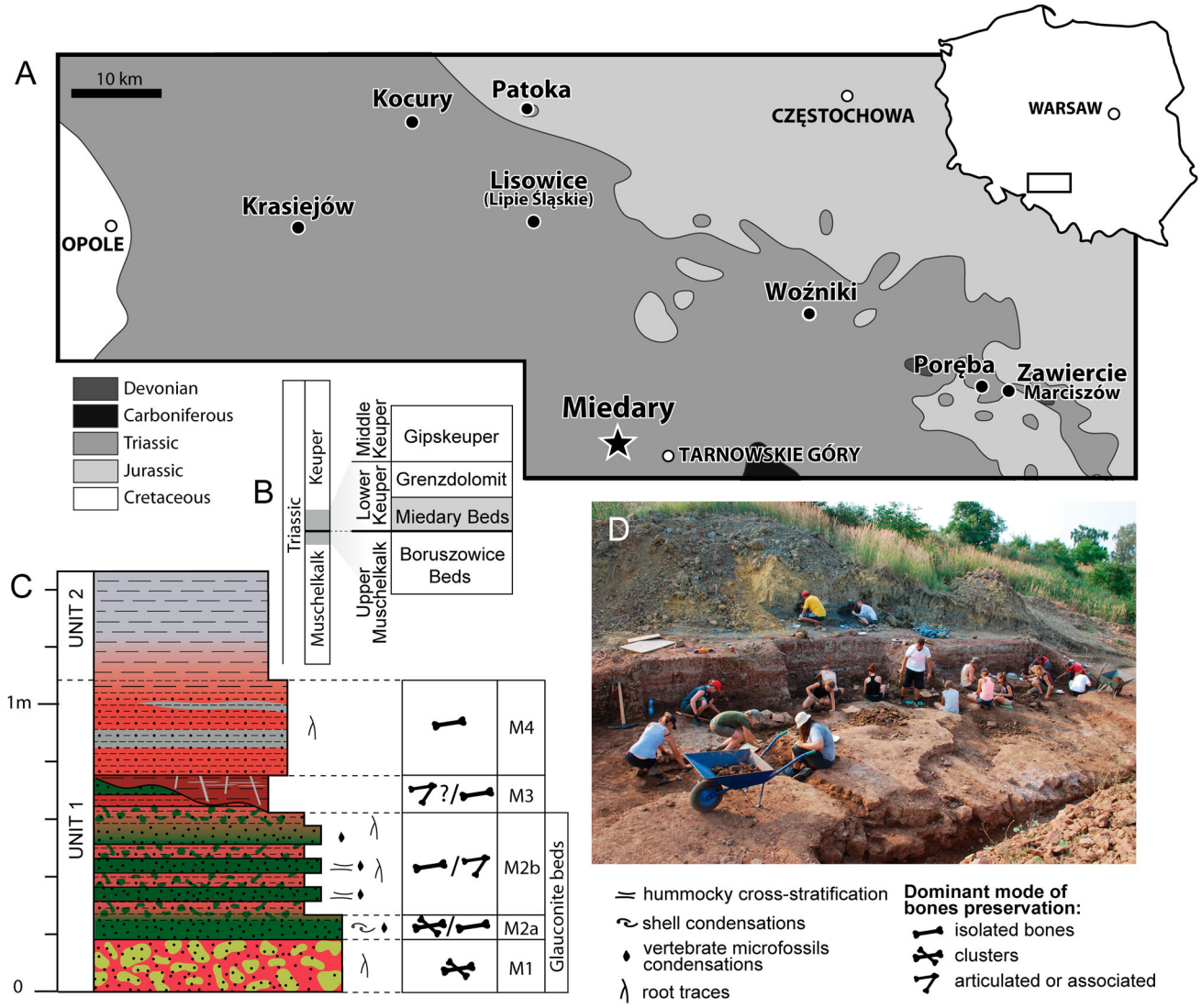

FIGURE 1. **A**, map of Poland with the main fossil-bearing Keuper localities in Silesia, (modified after Czepiński et al., 2021); **B**, placement of the Miedary Beds within the Triassic lithostratigraphic units of the Upper Silesia; **C**, geological section of the Miedary site; **D**, excavations in the Miedary claypit in 2015.

occur locally. Besides these features, the M3 layer exhibits a homogeneous structure. Bones and ichthyoliths appear to occur less frequently than in the glauconite beds but show a degree of articulation similar to the reddish, glauconite-poor facies in the M2b layer. However, the latter observation should be treated as preliminary, since significantly fewer specimens were collected from this bed. Above the M3 layer occurs a package of light-red sediment with gray-colored zones (M4). The vertebrate bones in this layer are very rare and occur as isolated specimens.

A reliable environmental interpretation of the bone-bearing sediments requires more detailed research on sediment features and fossil content. The studies focusing on depositional environments and taphonomy of the site are in preparation. Here we provide a preliminary interpretation based on field observations. The common occurrence of the glauconite and quartz grains in the glauconite beds points to formation of the entire package under marine conditions affected by a strong influx of terrigenous material. Nevertheless, the vertical diversity of this sequence is evidence for a changing bathymetry and energy of the environment. An informative character for the preliminary interpretation is the content and distribution of glauconite. The lowermost layer (reddish to yellowish sandstone) appears to be strongly altered by pedogenic processes since lamination is unreadable and thick root traces are common. The relatively low content of glauconite suggests that it may represent very proximal facies, possibly a tidal flat. The deposition of the following green glauconitic sandstone reflects transgression and deposition in a deeper zone influenced by an intense delivery of the glauconite grains. Contrary to other facies, in this layer fractured bones, bony particles, and disarticulated shell accumulations occur. This suggests a turbulent transport or intense reworking of the sediment. The subsequent depletion of the glauconite content in the reddish mudstones suggests reappearance of the shallower conditions. The higher articulation of fossils and lack of shell conglomerates indicate relatively calm sedimentation interrupted by high energy events evidenced by the glauconite-rich interbeds. The hummocky-cross-stratified interbeds point to the deposition of this part of the section close to the storm wave base. A comparative analysis of fish microfossils from this package showed lack of taxa occurring in the Germanic Basin deposits formed under fully marine salinities (Pawlak et al.,

2022), such as *Palaeobates* sp., *Colobodus* sp., and *Hybodus plicatilis*. The taxonomic composition of both fishes and tetrapods does not appear to vary vertically within the glauconite beds section. A different situation can be observed in the case of the M3 layer, which contains remains of an enigmatic reptile so far unknown from the glauconite beds. This layer was formed under more terrestrial conditions that is supported by the lack of glauconite and presence of the numerous gray-colored zones. The latter suggests subaerial exposition of this layer, and development of pedogenic processes. The connection with the open sea seems to be restricted based on the lack of unambiguous remains of marine reptiles. Conversely, a preliminary examination of microfossils suggests at least temporal influences of a marine environment, due to the presence of similar ichthyolith assemblage as in the glauconite beds. Unfortunately, they are relatively rare in this bed.

The exact age of the bone-bearing deposits in Miedary remains unclear due to the lack of index fossils, except for palynomorphs (Sulej et al., 2011). Pawlak et al. (2022) assessed the age of the Miedary deposits as early Ladinian (Fassanian). It was based on the synthetic comparison of the results of magnetostratigraphic and biostratigraphic studies, which provided a consistent lower constraint for the age of Miedary Beds. The paleomagnetic zone correlation indicates that the deposition of the Lower Keuper in Upper Silesia started after the early Fassanian (Nawrocki & Szulc, 2000). The studies on biostratigraphy of the Upper Silesian Muschelkalk demonstrated that the youngest ceratite zone preceding deposition of the Lower Keuper (the *spinosus* zone; Salamon et al., 2003) should also be correlated with the early Fassanian (Franz et al., 2013). The close proximity of the Laryszów outcrop, which represents this zone, suggests that the layers from the Miedary site are not significantly younger.

MATERIAL AND METHODS

The nomenclature of actinopterygian skull bones is based on the homology with sarcopterygians (Schultze, 2008). For the systematic position of tanystropheids, we followed Spiekman et al. (2021). The individual rarefaction analysis of data on the specimens collected from the Miedary site was performed in the PAST v.3.20 software (Hammer et al., 2001).

Specimens examined personally by the authors for comparative purposes: *Blezingeria ichthyospondyla* Fraas, 1896 vertebrae (SMNS, 7 specimens, W. P.; PIMUZ, 8 specimens, A. R.), *Bystrowiana permira* Vjushkov, 1957 vertebra with osteoderm (PIN 1100/4, Ł. C.), a number of cranial specimens (originals and molds) of *Mastodonsaurus cappelensis* (Wepfer, 1922) (holotype without given number and SMNS 7957, T. Sz.), *M. giganteus* Jaeger, 1828 (SMNS 4698, SMNS 4707, SMNS 7400, SMNS 54677, SMNS 54678, SMNS 54679, SMNS 80704, SMNS 81368, SMNS 92128, GPIT-PV-41172, T. Sz.), and '*M.*' *torvus* Konzhukova, 1955 (PIN 2867/67, T. Sz.), *Gerrothorax pustuloglomeratus* (SMNS, 13 specimens, T. Su.), *Plagiosuchus pustuliferus* (SMNS, 4 specimens, T. Su.), procolophonoid humeri (SMNS 91753, SMNS 92100, T. Sz.), *Tanystropheus* (GPIT, 46 specimens; MHI, 24 specimens; PIMUZ, 42 specimens; SMNS, 113 specimens, A. R.), *Serrolepis suevicus* Dames, 1888, scales (SMNS, 24 specimens, W. P.), upper jaws (SMNS, 10 specimens, W. P.), and articulated skeletons (SMNS, 6 specimens, W. P.), jaw bones of undetermined actinopterygians from the Vellberg locality (SMNS, 4 specimens, W. P.), and fish-bearing plates from the Vitriolschiefer (SMNS, 6 specimens, W. P.).

Institutional Abbreviations—**GPIT**, Geologisch-Paläontologisches Institut, University of Tübingen, Tübingen, Germany; **MHI**, Muschelkalkmuseum Hagdorn, Ingelfingen, Germany; **PIMUZ**, Palaeontological Institute and Museum, University of Zürich, Zürich, Switzerland; **PIN**, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order HYBODONTIFORMES Maisey, 1975

Four hybodontiform species were described from the glauconite beds by Pawlak et al. (2022): *Acrodus* cf. *A. lateralis* (Fig. 2A), *Lissodus nodosus* (Fig. 2F), *Polyacrodus keuperianus* (Fig. 2B), and *Polyacrodus* cf. *P. polycyphus* (Fig. 2C).

HYBODONTIFORMES indet.
(Figure 3B)

Material—Incomplete fin spine (ZPAL V. 36/611).

Stratigraphic Occurrence—M1–M2 layers (glauconite beds).

Description—The specimen represents an incomplete distal part of a spine, as suggested by its relatively thick walls and a narrow pulp cavity. The majority of the preserved portion of the spine is ornamented with longitudinal, enameloid-covered ridges. The posterior surface bears two longitudinal rows of spiny tubercles. One of them fades away distally. The tubercles are mostly eroded, thus estimation of their former properties is hampered.

Remarks—The described fin spine is the best-preserved specimen among several excavated from the Miedary site. All of them show similar morphology, typical for Hybodontiformes (see: Cappetta, 2012). The assignment of the spines to any particular species is difficult, since at least four species of hybodontiforms were recognized from the glauconite beds according to the studies on the teeth record (Pawlak et al., 2022). None of the excavated spines represent a tubercular ornament, undermining the interpretation of small bone particles with such ornamentation as fin spines fragments (Pawlak et al., 2022).

Class OSTEICHTHYES Huxley, 1880

Six taxa of bony fish were described from the glauconite beds by Pawlak et al. (2022): cf. *Gyrolepis* sp. (Fig. 2D, G), cf. Redfieldiiformes (Figs. 2H, 3D), *Saurichthys* sp. (Figs. 2E, 3A), *Serrolepis suevicus* (Figs. 2I, 3C, E), '*Thelodus*' sp., and *Ptychoceratodus* sp. (Fig. 2J).

Subclass ACTINOPTERYGII Cope, 1887
Order SAURICHTHYIFORMES Aldinger, 1937
Genus *SAURICHTHYS* Agassiz, 1834
SAURICHTHYS sp.
(Figs. 2E and 3A)

Material—Rostral fragment of the upper jaw (ZPAL V. 36/741), isolated tooth (ZPAL V. 36/742).

Stratigraphic Occurrence—M1–M2 layers (glauconite beds).

Description—The preserved part of the jaw is 7.9 cm long and consists of the anterior portion of the rostro-premaxillary with vomers. Its proximal end was found broken in the sediment. The distal portion of the jaw is flattened dorsoventrally and ornamented on the external dorsal side by ridges parallel to the long axis of the jaw. In the proximal direction, the flattening becomes lateral, whereas ornament on the lateral sides of the rostrum changes firstly into strongly undulating ridges, and subsequently into loosely arranged tubercles. Three morphotypes of teeth can

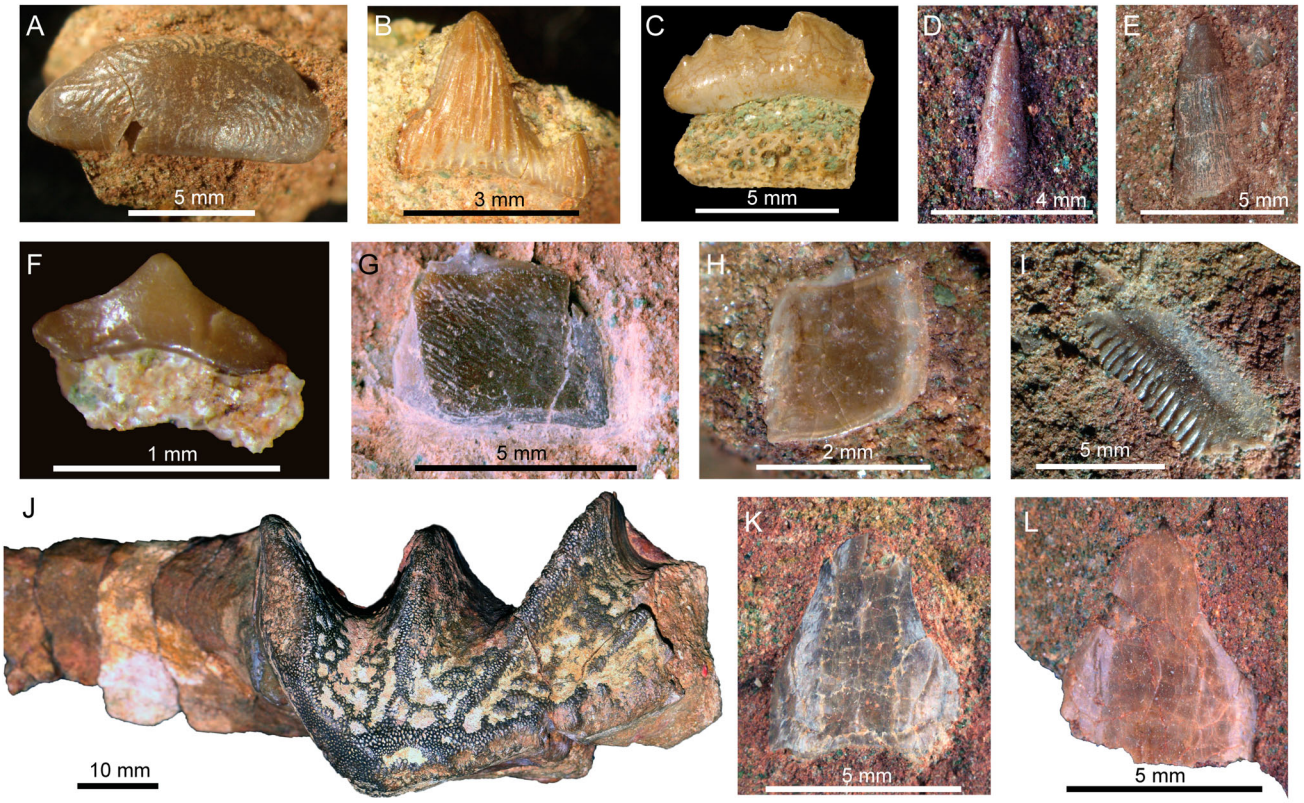

FIGURE 2. Fish remains from the Middle Triassic (Ladinian) of Miedary, Poland. **A**, *Acrodus* cf. *A. lateralis* Agassiz, 1839, ZPAL V. 36/624, isolated tooth; **B**, *Polyacrodus keuperianus* (Winkler, 1880), ZPAL V. 36/650, isolated tooth; **C**, *Polyacrodus* cf. *P. polycyphus* (Agassiz, 1843), ZPAL V. 36/604, isolated tooth; **D**, cf. *Gyrolepis* sp. Agassiz, 1835, ZPAL V. 36/780, isolated tooth; **E**, *Saurichthys* sp. Agassiz, 1834, ZPAL V. 36/742, isolated tooth; **F**, *Lissodus nodosus* Seilacher, 1943, ZPAL V. 36/09/27, isolated tooth; **G**, cf. *Gyrolepis* sp. Agassiz, 1835, ZPAL V. 36/783/01, isolated scale; **H**, cf. Redfieldiiformes ZPAL V. 36/792/01, isolated scale; **I**, *Serrolepis suevicus* Dames, 1888, ZPAL V. 36/703, isolated scale; **J**, *Ptychoceratodus* sp. Jaekel, 1926, ZPAL V. 36/700A, lower right dental plate in occlusal view; **K**, cf. *Prohalecites porroi* (Bellotti, 1857) ZPAL V. 36/1900, skull roof in dorsal view; **L**, cf. *Prohalecites porroi* (Bellotti, 1857) ZPAL V. 36/1901, skull roof in dorsal view.

be distinguished. The first are large, conical teeth, with two cutting edges, conspicuous apicobasal ridges, and a high acrodin cap. They are distributed along the rostro-premaxillary margins in roughly regular distances. The second morphotype is represented by smaller teeth, but generally similar to the first morphotype, distributed randomly between the larger ones. The third morphotype, occurring mainly on the vomers, consists of low, button-like teeth with blunted acrodin caps.

Remarks—*Saurichthys* rostral fragments are among the most common cranial fish fossils from the Middle Triassic of the Germanic Basin. Unfortunately, they are predominantly too fragmentary for more detailed comparisons. The numerous, heavy teeth exceed, or roughly equal, the height of the corresponding part of the jaw. This is a shared character of ZPAL V.36/741 and *S. costasquamosus* from the Ladinian of the Monte San Giorgio area (Rieppel, 1985; Tintori, 2019). The teeth similar to the first morphotype have been identified from the same bed as isolated specimens (Pawlak et al., 2022).

Order REDFIELDIIFORMES Berg, 1940
REDFIELDIIFORMES indet.
(Figs. 2H and 3D)

Material—Part of the right pectoral girdle, comprising an almost complete cleithrum with an attached supracleithrum fragment (ZPAL V. 36/790), isolated scale (ZPAL V. 36/792/01).

Stratigraphic Occurrence—M1–M2 layers (glauconite beds), M3.

Description—The specimen is preserved on a rock surface and exposed from the medial side. The cleithrum has prominent ventral and dorsal processes, which enclose a roughly right angle. The tip of the ventral process is broken, and no suture for the clavicle is visible. The branchial lamina originates as a medially oriented ridge running along the ventral process, and reaches its maximum width close to the base of the dorsal process, which appears to be almost entirely formed by the branchial lamina. In the mesial view, the maximum width of the branchial lamina is roughly equal to the maximum width of the lateral lamina. The posterodorsal margin of the dorsal process forms an elongated suture with the supracleithrum. It is a robust bone with the maximal width larger than the total width of the cleithrum in any section. It has a slightly concave medial surface. The posterior edge of the supracleithrum is smooth, whereas the posteroventral edge of the cleithrum is not preserved. The specimen is damaged in its dorsal and posterior portions, and imprints of the lateral surfaces of both bones are exposed. They reveal an ornament composed of robust, slightly undulating, longitudinally oriented ridges.

Remarks—A wide supracleithrum and a heavy sculptured pectoral girdle are characters common among Redfieldiiformes (Gibson, 2018; Schaeffer, 1984). These fish were small, fusiform predators, occurring predominantly in freshwater deposits. It is consistent with the roughly equal lengths of cleithrum processes, suggesting a fusiform shape of its owner's body. The presence of redfieldiiforms in the glauconite beds at Miedary is partially supported by smooth redfieldiiform-like scales, occurring

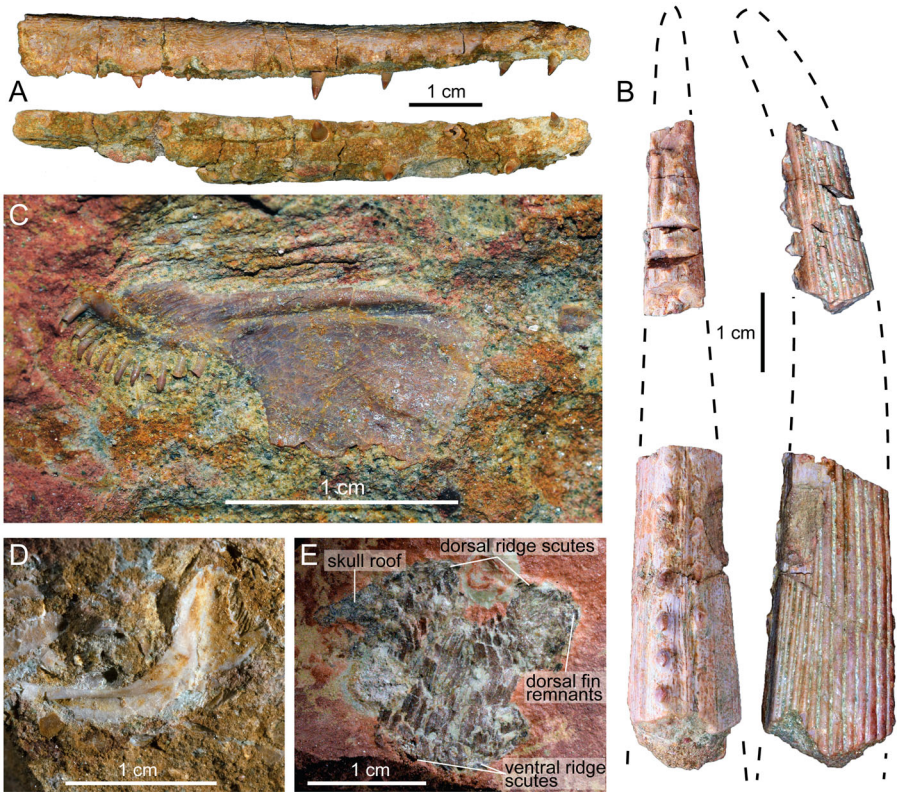

FIGURE 3. Fish remains from the Middle Triassic (Ladinian) of Miedary, Poland. **A**, *Saurichthys* sp., ZPAL V. 36/741, upper jaw in left lateral and occlusal views; **B**, Hybodontiformes indet., ZPAL V. 36/611, incomplete fin spine in posterior and right lateral views; **C**, *Serrolepis suevicus* Dames, 1888, ZPAL V. 36/721, upper jaw in medial view; **D**, Redfieldiiformes indet., ZPAL V. 36/790, right cleithrum in medial view; **E**, *Serrolepis suevicus* Dames, 1888, ZPAL V. 36/722, partial articulated skeleton compacted laterally.

abundantly as isolated elements (Pawlak et al., 2022). However, it is worth noting that such scale morphology is not unique for this group. Regrettably, the record of Middle Triassic redfieldiiforms is scarce in the Germanic Basin. It comprises mostly isolated bones and undescribed individuals of possible redfieldiiforms from the Lower Keuper of Germany (Böttcher, 2015).

Order PERLEIDIFORMES Berg, 1940
Family POLZBERGIDAE Griffith, 1977
Genus *SERROLEPIS* Dames, 1888
SERROLEPIS SUEVICUS Dames, 1888
(Figs. 2I and 3C, E)

Material—Articulated skeleton (ZPAL V. 36/722), upper jaw with associated scales (ZPAL V. 36/721), isolated scale (ZPAL V. 36/703).

Stratigraphic Occurrence—M1–M2 layers (glauconite beds), M3.

Description—ZPAL V. 36/722 is an articulated but incomplete specimen of a deep-bodied fish. It comprises the skull roof and anterior and middle portions of the trunk. The body outline is roughly round; however, the morphology of the posteriormost part of the trunk remains unknown. The preserved part of the trunk is covered with about 12 vertical rows of high scales, exposed from the medial side. Some of them have a visible dorsal peg. Ridge scales occur along the dorsal and ventral sides of the specimen. The dorsal scutes are fusiform in the lateral aspect and strongly elongated, whereas the ventral scutes are roughly isometric triangular in the lateral aspect. In the posterodorsal part of the specimen, an undetermined number of rhombic scale rows is present, accompanied by radials, representing a posteriorly located dorsal fin. The skull roof is triangular, with a tubercular ornament. Unfortunately, the state of preservation impedes a detailed examination of the specimen. The back and pectoral girdle are strongly damaged by piercing sand-filled burrows.

In ZPAL V. 36/721, the isolated upper jaw is exposed from the medial side. It is composed of the firmly fused maxilla and premaxilla. The anterior region of the premaxilla is anteriorly elongated, medially curved, and forms the symphyseal contact for the contralateral premaxilla. Posteriorly, the premaxilla has two processes. The posteroventral process forms the occlusal margin of the jaw, whereas the posterodorsal process runs posteriorly, alongside the dorsal margin of the maxilla. The posterodorsal process is about 12 times longer than the posteroventral process. Teeth occupy the entire ventral margin of the premaxilla. The maxilla is a flat bone with a rectangular and strongly expanded ventrally posterior portion. It has a triangular anterior process, inserted between the posteroventral and the posterodorsal processes of the premaxilla. Ventrally to the dorsal suture with the premaxilla, a horizontal longitudinal ridge is located. Twelve teeth are present on the premaxillary occlusal edge, whereas the maxilla is toothless. The teeth are high, pencil-like, with blunted acrodin caps ornamented with barely visible minute, apicobasal ridges. The height of the teeth decreases posteriorly. The jaw is associated with two deep scales. They are three times higher than wide, exposed from the medial side, and have a conspicuous peg-and-socket system.

Remarks—Isolated scales and teeth of *Serrolepis suevicus* have previously been reported from the Miedary site (Pawlak et al., 2022). They are indistinguishable from other *S. suevicus* scales from the Lower Keuper deposits (Serrolepisbank, Untere Graue Mergel, Sandige Pflanzenschiefer, and Estherienschichten [Böttcher, 2015; Dames, 1888; Hagdorn & Mutter, 2011]). The specimen ZPAL V. 36/721 further supports the presence of this species in Miedary. The premaxilla fused with maxilla, elaborate posterior process of premaxilla, and pencil-

like teeth are characters diagnostic for the Polzbergidae (compare: Griffith, 1977; Lombardo & Tintori, 2004; Lombardo et al., 2008; Sun et al., 2009). A difference is the rectangular maxilla, which is usually triangular in polzbergids. However, a similar, rectangular posterior field of maxilla can be observed in isolated maxillae originating from the Serrolepisbank and Untere Graue Mergel and referred to *Serrolepis* (W. P. pers. obs.). This character is especially evident in the specimen MHI 1748/13 from Serrolepisbank, an articulated individual, which exhibits the rectangular maxilla (Hagdorn & Mutter, 2011:fig. 5e). ZPAL V. 36/722 serves as evidence for the taphonomic conditions allowing the preservation of fish bodies in articulation during the deposition of the glauconite beds. The body shape of ZPAL V. 36/722, its scalation, and ornamentation of skull roof are consistent with a deepened morphotype of *S. suevicus* from the western part of the Basin (Böttcher, 2015; Hagdorn & Mutter, 2011). However, no unambiguous features can support its identification as *Serrolepis* except the morphology of scales. The latter is nonetheless an important diagnostic feature, since no material other than scales was used for the original description of this taxon (Dames, 1888). Several other actinopterygians known from the Middle Triassic show the upper jaw shape, dentition, and scales similar to polzbergids: *Ctenognathichthys bellottii* and *Louwoichthys pusillus* (see: De Alessandri, 1910; Tintori, 1998; Xu, 2021). Both show significantly higher teeth, exceeding several times the height of the anterior part of the upper jaw. Scales of *L. pusillus* have significantly weaker serration than those from Miedary. The profile of the upper jaw behind the dentigerous part is convex in *C. bellottii*, unlike in the *S. suevicus* specimens from Germany and Miedary. Scales referred to as *S. suevicus* have also a significantly higher ratio of height to width than *C. bellottii.* Moreover, *L. pusillus* shows weaker serration on scales than *S. suevicus.* However, the entire group requires revision with special focus on interspecific variation, which for *S. suevicus* appears to be significant (Hagdorn & Mutter, 2011).

Infraclass TELEOSTEOMORPHA Arratia, 2001
cf. *PROHALECITES PORROI* (Bellotti, 1857)
(Fig. 2K–L)

Material—Skull roofs (ZPAL V. 36/1900, ZPAL V. 36/1901).

Stratigraphic Occurrence—M1–M2 layers (glauconite beds), M3.

Description—The paired parietals are elongated anteroposteriorly, about twice as long as wide. They narrow anteriorly with an abrupt change of width at mid-length. In ZPAL V. 36/1901, the anterior border of parietals appears to be slightly protruded along the midline. The suture between the parietals is developed as straight to deeply anastomosing. Posterior, the parietals articulate with the postparietals, which are paired in ZPAL V. 36/1900, and merged into one plate in ZPAL V. 36/1901. When paired, they are flat, rectangular bones, slightly elongated in the mediolateral direction. Posteriorly to the postparietals, three extrascapulars are located, but are not preserved in ZPAL V. 36/1901. The extrascapulars, postparietals, and parietals suture to the dermopterotics, which are firmly attached to the rest of the skull roof. The dermopterotics in ZPAL V. 36/1901 show an ornament composed of anastomosing ridges running anteroposteriorly. The supraorbital sensory line runs anteroposteriorly through the middle of the parietals, and continues onto the postparietals. The supratemporal sensory line is visible on the right dermopterotic of ZPAL V. 36/1901, and runs anteroposteriorly. All bones are covered by a continuous layer of ganoine, unornamented besides the dermopterotics.

Remarks—Isolated skull roofs of actinopterygians occur relatively often in the glauconite beds. Their total length varies from 6.5–9 millimeters. Despite some anatomical variation (merging of the postparietals, shape of the mesial suture), all found specimens represent the same pattern of bone composition and ornamentation. The elongated parietals with expanded posterior portions, scarce ornamentation, and expanded, trapezoidal dermopterotics point to their teleosteomorph affinity. Various patterns of the skull roof bones merging occur in the early representatives of this group and early holosteans as well (Arratia, 2013; Arratia & Herzog, 2007; Tintori et al., 2015). The specimens from Miedary are most similar to *Prohalecites porroi* from the upper Ladinian of the Monte San Giorgio region (De Alessandri, 1910; Tintori, 1990). The similarities concern the shape, ornamentation, and the sensory lines trajectory in all bones preserved in the specimens from Miedary. The exception are postparietals which are slightly elongated anteroposteriorly in *P. porroi*, whereas in the described material they tend to be isometric or even elongated laterally. Similar to *Prohalecites* from the Monte San Giorgio area, the postparietals are occasionally fused (Tintori, 1990). Early neopterygians are represented in the Lower Keuper deposits by articulated specimens assigned to *Prosantichthys* (Böttcher, 2015) but none of the examined or figured individuals exposes a skull roof (W. P. pers. obs.). The more complete specimens from the Prosanto Formation show strong fusion of the skull roof bones, which does not occur in the specimens from Miedary (Arratia & Herzog, 2007).

Class AMPHIBIA Gray, 1825
Order TEMNOSPONDYLI Zittel, 1887
Family MASTODONSAURIDAE Lydekker, 1885
Genus *MASTODONSAURUS* Jaeger, 1828
MASTODONSAURUS sp.
(Fig. 4A)

Material—ZPAL V. 36/301, a nearly complete skull.

Stratigraphic Occurrence—M1–M2 layers (glauconite beds), M3, M4.

Description—The skull is nearly complete, although the middle and right portions of the postorbital area were destroyed during recovery. It is 59 cm long and 38 cm wide. This results in a complete length to width ratio equal to 1.55, noticeably larger than in *M. giganteus*, in which this ratio does not seem to exceed 1.35 (Damiani, 1999; Schoch, 1999; T. Sz. pers. obs. 2016). The skull is slightly compacted concordant with its anatomical flattening, and we regard the compaction influence on measurements presented herein negligible. Despite damage, the sutural pattern is mostly discernible and virtually the same as in *Mastodonsaurus cappelensis* and *M. giganteus* (e.g., Damiani, 2001; Moser & Schoch, 2007; Schoch, 1999; Wepfer, 1923). Large, subovoid tusk holes are mostly surrounded by the premaxillae, but the nasals contribute to their posteromedial edges. The nasal flexures of the supraorbital sensory canals are distinct, and each takes a form of two sharp (over 90°) turns posteromedial to the nares. Likewise, the lacrimal flexures are very distinct. The sensory canals are generally well defined and easily distinguishable from the surrounding sculpturing, although at the level of the nasal flexures and the anteriormost ends, the supraorbital sensory canals are transversely crossed by low ridges, less pronounced than the ridges of the surrounding ornamentation. The orbits were at least 12 cm long. Their general outline is ovoid, with the distinct anterior constriction typical for *M. giganteus* (e.g., Schoch, 1999). The orbits are located entirely in the posterior half of the skull, like in *M. cappelensis* and relatively more posteriorly than in *M. giganteus* (Damiani, 2001; Schoch, 1999). Despite damage, the widths of both the interorbital and jugal bars are clearly smaller than the orbit width; they are certainly narrower than in *M. cappelensis* but the difference is less pronounced than in *M. giganteus*

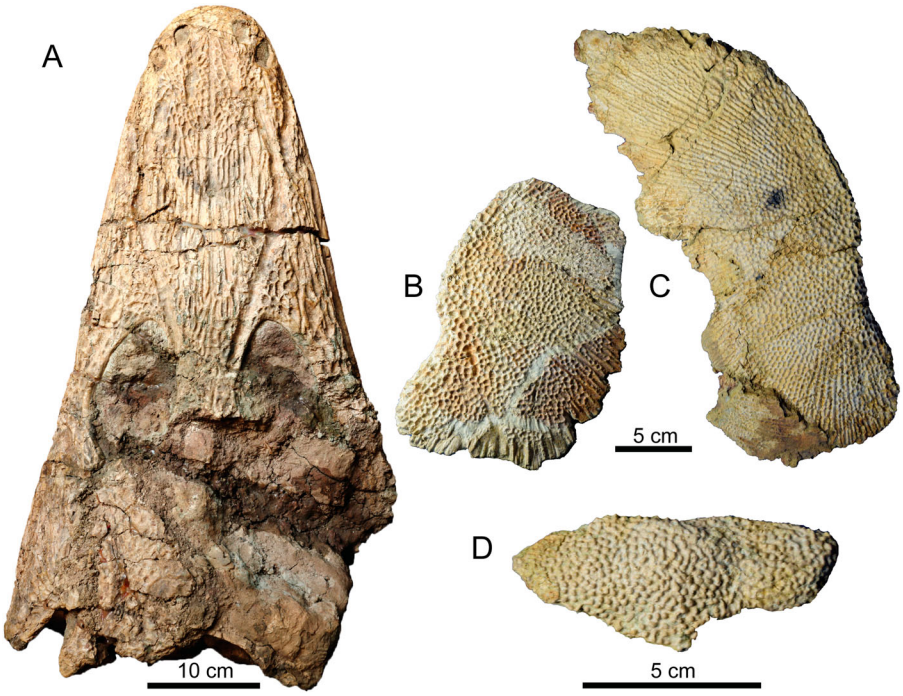

FIGURE 4. Temnospondyl remains from the Middle Triassic (Ladinian) of Miedary, Poland. **A**, *Mastodonsaurus* sp., ZPAL V. 36/301, nearly complete skull in dorsal view; **B**, Plagiosterninae indet., ZPAL V. 36/356, right clavicle in ventral view; **C**, *Plagiosternum* sp., ZPAL V. 36/353, left clavicle in ventral view; **D**, cf. *Gerrothorax* sp., ZPAL V. 36/355, right cleithrum in lateral view.

(Damiani, 2001; Schoch, 1999; Wepfer, 1923). The otic (squamosal) notch is widely open. The tabular horn is directed posterolaterally and ends bluntly. The quadrate rami of the pterygoids are short but directed more posterolaterally than in *M. cappelensis* and *M. giganteus*, and the quadrate condyles extend further posteriorly than the occipital condyles rather than being level (Damiani, 2001; Schoch, 1999; Wepfer, 1923). The posterior part of the basal plate of the parasphenoid is cracked, which makes the morphology of the fossa parasphenoidalis and the opening of the Eustachian tube ambiguous. Nonetheless, as is typical for *M. giganteus*, the parasphenoid is posterolaterally expanded (Damiani, 2001; Moser & Schoch, 2007; Schoch, 1999).

Remarks—Kunisch (1885) described a partial mandible from the Muschelkalk of Zakrzów (his Sacrau) near Gogolin, Poland, as *Mastodonsaurus silesiacus* Kunisch, 1885, but this find was considered by later authors (Damiani, 2001; Schoch, 1999; Schroeder, 1913) a *nomen dubium*, likely a representative of *Parotosuchus* or possibly some other capitosauroid genus. Due to the temporal difference between that specimen and the material from Miedary, as well as due to its undiagnostic morphology, we follow this assumption and consider it distinct from *Mastodonsaurus* from Miedary.

Family PLAGIOSAURIDAE Jaekel, 1914
Subfamily PLAGIOSTERNINAE Shishkin, 1986
Genus *GERROTHORAX* Nilsson, 1934
cf. *GERROTHORAX* sp.
(Fig. 4D)

Material—ZPAL V. 36/355, right cleithrum.
Stratigraphic Occurrence—M1–M2 layers (glauconite beds).
Description—The well-preserved cleithrum (Fig. 4D) is complete but the tip of the processus clavicularis might be slightly broken. The anteroposteriorly extended cleithral head is thick and covered with tubercles. The tubercular ornamentation is well visible on its lateral side and consists of small irregular tubercles, characteristic for *Gerrothorax* spp., *Plagiosuchus* and *Plagioscutum* (Hellrung, 2003; Huene, 1922; Jenkins et al., 2008; Schoch & Witzmann, 2012; Shishkin, 1986). The ornamented part is bean-shaped. A triangular processus clavicularis is visible on the medial side. The crista medialis is oblique to the dorsal edge.

Remarks—The overall cleithral structure strongly corresponds to that described and illustrated by Huene (1922: fig. 34), Nilsson (1945), Shishkin (1987:fig. 29), and Jenkins et al. (2008) for *Gerrothorax pulcherrimus* Huene, 1922, which shows considerable large variability of shapes (T. Su. pers. obs.). ZPAL V. 36/355 fits within this variability, yet with some notable differences. In the Miedary specimen, the crista medialis is posterodistally oblique to the dorsal edge whereas in *Gerrothorax pulcherrimus* it is oblique or perpendicular. The clavicularis area is much larger than the scapularis area, and their dorsal edges are not as distinct as in some specimens of *Gerrothorax* (e.g., SMNS 83088). According to Schoch and Milner (2014), plagiosaurines (= *Gerrothorax* + *Plagiosaurus*) have a similar pustulate ornamentation. The cleithrum of *Plagiosaurus* is unknown. The interclavicle of *Plagiosuchus* also has dermal sculpture consisting of pustules, but the general shape of the interclavicle and clavicle is very different from in Plagiosaurinae, so it is likely that the cleithrum also might be different.

Genus *PLAGIOSTERNUM* Fraas, 1896
PLAGIOSTERNUM sp.
(Fig. 4C)

Material—ZPAL V. 36/353, left clavicle.
Stratigraphic Occurrence—M1–M2 layers (glauconite beds).
Description—The specimen (ZPAL V. 36/353; Fig. 4C) represents a left clavicle. The clavicle plate is almost complete, although the medial edge is damaged and the tip of the dorsal process is broken. The plate is elongated, with the dorsal process located in the central part but closer to the posterior end. The lateral edge is sinusoidal with its concave part occupying the posterior quarter of the edge. The clavicle ZPAL V. 36/353 has a sculpture that consists of isometric pits and grooves. In

some areas, the border between the pits and grooves is not well defined.

Remarks—The sculpture observed in the specimen ZPAL V. 36/353 is different from in *Plagioscutum ochevi* Shishkin 1986, *Plagiosuchus pustuliferus* Fraas 1896, *Plagiorophus danilovi* Shishkin 1986, and *Plagiorophus paraboliceps* Konzhukova 1955 (Fraas, 1889; Shishkin, 1987:pl. 6, figs. 15–16) in the lack of any tubercles. The size of the posterior part of the dorsal process of the clavicle is highly variable in the Plagiosterninae. That part is very long in *Plagioscutum ochevi*, middle-sized in *Plagiosternum granulosum* and ZPAL V. 36/353, and very short or absent in *Plagiorophus danilovi* and *Plagiorophus paraboliceps* (Fraas, 1913; Shishkin, 1987). The anterior convexity is very subtle in the specimen from Miedary as in *Plagiosternum granulosum* Fraas, 1913 (see Fraas, 1913:pl. 17, fig. 2). *Melanopelta antiqua* exhibits a more massive plate and dorsal process although this difference might be connected with ontogeny (Shishkin, 1987). The sculpture of ZPAL V. 36/353 is similar to the partially preserved clavicle of *Plagiosternum granulosum* (see Fraas, 1913:pl. 17, fig. 2); however, in contrast to the latter, the plate of ZPAL V. 36/353 is ornamented only ventrally.

PLAGIOSTERNINAE indet.
(Fig. 4B)

Material—ZPAL V. 36/356, right clavicle; ZPAL V. 36/354 and ZPAL V. 36/357, two left clavicles.

Stratigraphic Occurrence—M1–M2 layers (glauconite beds).

Description—The most informative specimen (ZPAL V. 36/356; Fig. 4B) represents a right clavicle. Its plate is almost complete, only the anterior edge is broken and the dorsal process has its top damaged. The sculpture is similar to *Plagiosternum granulosum* (Fraas, 1913:pl. 17, fig. 2), but the plate is very short, with a straight posterior edge (also in both ZPAL V. 36/354 and 357), and the dorsal process is placed in the middle part (not posteriorly like in *Plagiosternum granulosum*). The lateral edge is sinusoidal with a concave part placed along the posterior 1/3 of its length. The anterior convexity is very distinct, differing from ZPAL V. 36/353 and *Plagiosternum granulosum* (Fraas, 1913:pl. 17, fig. 2). The clavicle ZPAL V. 36/356 has a sculpture consisting of isometric pits and grooves present only along its anteromedial and posteromedial edge.

Remarks—The sculpture does not have any tubercles, in contrast to *Plagioscutum ochevi*, *Plagiosuchus pustuliferus*, *Plagiorophus danilovi*, and *Plagiorophus paraboliceps* (Fraas, 1889; Shishkin, 1987:pl. 6, figs. 15, 16). In ZPAL V. 36/356 the posterior part of the plate (behind the dorsal process) is mid-sized like *Plagiosternum granulosum*. *Melanopelta* has a more massive plate and dorsal process (Shishkin, 1987). ZPAL V. 36/356 differs from ZPAL V. 36/353 in a short anterior part of the plate, sculpture with larger pits despite a similar width of the clavicles, very concave anterior part of the lateral edge, and the presence of a long and deep groove that looks like a sinusoidal sensory line in the posterior part of the sculptured area (in two specimens ZPAL V. 36/356 and ZPAL V. 36/354 with visible sculpture of that type the sinus looks similar). A similar sinus of the sensory line was described in *Dutuitosaurus ouazzoui* (Dutuit, 1976). There is an area without a typical sculpture of pits and grooves, which is located on the ventral part of the plate, close to the posterior edge. It is covered with ridges which are perpendicular to the edge. Such a sculpture is limited to the ventral part of the plate.

Order CHRONIOSUCHIA Tatarinov, 1972
Family BYSTROWIANIDAE Vjushkov 1957
Genus *BYSTROWIELLA* Witzmann, Schoch & Maisch, 2008
BYSTROWIELLA cf. *B. SCHUMANNI* Witzmann, Schoch & Maisch, 2008
(Fig. 5D)

Material—ZPAL V. 36/505, a complete osteoderm.

Stratigraphic Occurrence—M2 layer.

Description—The isolated osteoderm ZPAL V. 36/505 displays a butterfly-shaped morphology in dorsal view, which is typical for chroniosuchians (Novikov & Shishkin, 2000). It is 55 mm wide and 28 mm long. It consists of a dorsal plate and a posterior articular plate. The latter is located below the main (dorsal) osteoderm plate. This resulted in a dorsal overlapping of this element by the posteriorly following osteoderm. The dorsal ornamentation is formed by a series of elongated, transverse grooves, similar to those seen in *Bystrowiella schumanni* Witzmann et al., 2008; lacking the parasagittal ridges observed in *Chroniosuchus paradoxus*, *Chroniosaurus* spp., *Jarilinus mirabilis,* and *Suchonica vladimiri* (Buchwitz et al., 2012; Golubev, 1998, 1999). The pustules, seen in *Chroniosaurus dongusensis* and *Madygenerpeton pustulatus*, are absent. Each wing of the dorsal plate of ZPAL V. 36/505 is transversely wide, with the width to length ratio being equal to 1.07, similar to the range reported for *Bystrowiella schumanni* SMNS 91034 (Witzmann et al., 2008), but wider than in *Synesuchus muravjevi* Novikov & Shishkin, 2000 PIN 4466/12 (with the ratio equal to 0.7; Novikov & Shishkin [2000]; however, these ratios seems to vary intraspecifically, see Witzmann & Schoch [2018]). The lateral edges of the lateral wings are relatively more convex in dorsal view in ZPAL V. 36/505 than in *B. schumanni* SMNS 91034 (see Witzmann et al., 2008); however, not to the degree seen in *S. muravjevi* PIN 4466/12 (see Novikov & Shishkin, 2000). The posterodorsal articulation facets are absent on the lateral wings of ZPAL V. 36/505, and the posterior articulate plate is divided into three processes, making it similar to the osteoderms of *Bystrowiana permira*, *Axitectum vjushkovi*, *S. muravjevi*, and *B. schumanni*. The medial process of the posterior articular plate is tubercle-like and is positioned well above the lateral ones, as in *B. schumanni* and *S. muravjevi*.

Remarks—Most chroniosuchians are known from the late Permian to Middle Triassic sediments of European Russia and China (Liu & Chen, 2020; Novikov & Shishkin, 2000). One exception is *Bystrowiella schumanni* from the Middle Triassic of Kupferzell and Vellberg (Germany; Witzmann et al., 2008). As expected, the morphology of ZPAL V. 36/505 is most similar to the material collected from the roughly coeval sediments from Germany. There are subtle differences between ZPAL V. 36/505 and the holotype specimen of *B. schumanni* (SMNS 91034), namely the transverse sculpture nearly reaching the lateral edges in the Miedary specimen; the lateral edges being more convex; the lateral wings being wider transversely; the presence of a subtle, dorsoventrally flat tubercle placed medially on the each of the lateral wings. However, our specimen fits within the range of variation established by the material referred to *B. schumanni* by Witzmann and Schoch (2018), so these differences are most likely a result of the intraspecific variation of the dermal armor in *Bystrowiella*.

Class REPTILIA Laurenti, 1768
Order PROCOLOPHONOMORPHA Romer, 1964
Family OWENETTIDAE Broom, 1939
OWENETTIDAE indet.
(Fig. 5E)

Material—Right humerus (ZPAL V. 36/508).

Stratigraphic Occurrence—M2 layer.

Description—The right humerus (ZPAL V. 36/508) is nearly complete and its length equals 5 cm. The angle between the proximal and distal heads is probably affected by compaction and it is

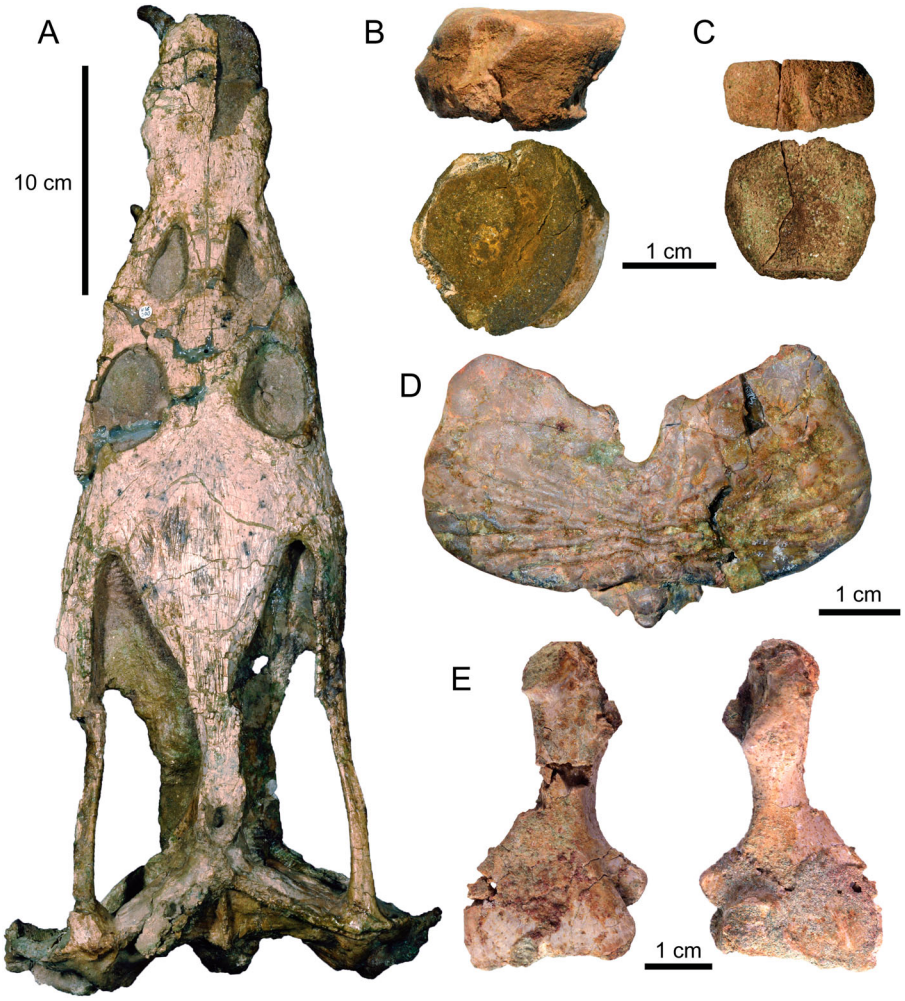

FIGURE 5. Tetrapod remains from the Middle Triassic (Ladinian) of Miedary, Poland. **A**, sauropterygian *Nothosaurus* sp., ZPAL V. 36/200, nearly complete skull in dorsal view; **B**, **C**, *Blezingeria* sp., ZPAL V. 36/518 (**B**) and ZPAL V. 36/517 (**C**), isolated vertebral centra in dorsal and posterior views; **D**, chroniosuchian *Bystrowiella* cf. *B. schumanni* ZPAL V. 36/505, an isolated osteoderm in dorsal view; **E**, Owenettidae indet. ZPAL V. 36/508, right humerus in dorsal and ventral views.

difficult to assess its original value. The proximal articular surface is bean-shaped. Its posterodorsal part is broader transversely than the ventral one, with a convex and rough surface. It is very close to the lesser tuberosity, separated only by a narrow, slightly concave strip of bone. The lesser tuberosity is a robust, distinct structure on the ventral aspect of the bone. The tuberosity is damaged posteriorly. It extends distally to form a subtriangular buttress process. The process is directed anteriorly and has a flat ventral surface. Additional convexities appear proximodorsally to the process. In contrast to the lesser tuberosity, the deltopectoral crest is much less robust. It is subtriangular and oriented anterodorsally. Its tip is slightly damaged but it is clear that the crest was relatively low. The deltopectoral crest, lesser tuberosity, and posterodorsal part of the articular surface are almost evenly distributed around the head in proximal view. The three structures are well separated by proximodistally elongate fossae. The humeral shaft is rather short, quickly expanding into the distal end. The shaft is quarter oval in cross section with the convex part on the posteroventral side. The distal end is flattened and significantly expanded anteroposteriorly, being 2.9 cm wide. The entepicondyle is proximodistally tall. Its posterodistal (mediodistal) edge is nearly straight and forms a right angle with the distal margin of the head. The entepicondylar foramen is absent. The ectepicondyle is thicker and more rounded than the entepicondyle, and it meets the open ectepicondylar notch that forms an anterodistal groove. The supinator process emerges proximoventral to the notch. The distal end is slightly concave in the dorsal aspect but otherwise almost featureless. It has a nearly straight distal margin. The ventral side bears a square capitellum (radial condyle) that extends proximally to the level of the supinator process. It merges posteriorly with the indistinct subtriangular trochlea (ulnar condyle).

Remarks—An open ectepicondylar notch of ZPAL V. 36/508 is diagnostic for Owenettidae (Martinelli et al., 2016; Reisz & Scott, 2002). ZPAL V. 36/508 differs from the humerus of *Saurodektes kitchingorum* in a larger degree of flaring of the distal end and apparently more distally placed deltopectoral crest (although note that the humeri-preserving individuals of *S. kitchingorum* are not fully ossified; Reisz & Scott, 2002) and from *Barasaurus besairei* Piveteau, 1955 in a less offset head and proportionately much larger distal end (Martinelli et al., 2016; McMenamin, 2018; Meckert, 1995). It is particularly similar to the unnamed owenettid humeri ("aff. *Barasaurus*") from the Ladinian of Germany, SMNS 92101 and SMNS 92100 (Martinelli et al., 2016). ZPAL V. 36/508 appears to have a much larger radial condyle than SMNS 92101 but probably similar to SMNS 92100. Most other differences between them, such as the width of the proximal head or torsion of the bone, could be attributed to taphonomic factors, especially to the strong dorsoventral compaction of ZPAL V. 36/508 and, even stronger, SMNS 92100. The three specimens may indeed belong to the same or closely related species. The only other owenettid known from the time range

comparable with that of the Miedary assemblage is *Candelaria barbouri* from the possibly roughly contemporary *Dinodontosaurus* Assemblage Zone of the Santa Maria Formation in southern Brazil (Philipp et al., 2018). Unfortunately, the hypodigm of *Candelaria barbouri* does not include humeri (Cisneros et al., 2004, 2006; Da Rosa et al., 2004; Müller, 2021; Price, 1947), and thus comparisons are not possible.

Order ?THALATTOSAURIA Merriam, 1904
Family INCERTAE SEDIS
Genus *BLEZINGERIA* Huene, 1951
BLEZINGERIA sp.
(Fig. 5B, C)

Material—Two vertebral centra (ZPAL V. 36/517 and ZPAL V. 36/518).

Stratigraphic Occurrence—M1–M2 layers (glauconite beds).

Description—The specimens are slightly eroded, but several characteristic anatomical features can still be noted. In the specimen ZPAL V. 36/517 the centrum is 5 mm long and its diameter equals about 17 mm. The specimen ZPAL V. 36/518 is larger, with the centrum being 13 mm long and having a diameter equal to about 23 mm. Both are amphicoelous without a trace of a notochordal pit. The anterior side of the vertebrae is semicircular, while the posterior side is flatter and ventrolaterally constricted. In ZPAL V. 36/517 two symmetrically placed articular facets are located high on the dorsoposterior portion of the lateral sides of the centrum. On the dorsal side of the centra, an anteroposteriorly oriented articular facet for the neural arch is present. It is rectangular, with an anteroposteriorly directed groove running through the middle of the facet. Broad and shallow depressions on the dorsolateral portion of the centra may represent the laterally directed neural arch articulation facet, although the state of preservation of the specimens precludes a definite interpretation. The ventral side of ZPAL V. 36/517 is anteroposteriorly expanded. Similar to what can be seen on the articular facets, the cancellous bone is exposed on the whole surface of the well outlined, flat and elliptical in shape ventralmost part of this specimen.

Remarks—Several disc-shaped, amphicoelous vertebral centra, very similar to ZPAL V. 36/517 and ZPAL V. 36/518, have been described from the Ladinian sediments of Germany (Diedrich, 2015; Fraas, 1896; Huene, 1951; Müller, 2002). These specimens were assigned to *Blezingeria*, an enigmatic marine reptile known only from isolated records (Müller, 2002). The first described specimens were assigned to a new *Nothosaurus* species by Fraas (1896). Huene (1951) redescribed this material as a new ichthyosaur genus —*Blezingeria*. Rieppel (1998) suggested thalattosaurian affinities for this taxon, but exact phylogenetic relationships of *Blezingeria* remain uncertain (Müller, 2002; Schoch, 2015). A discussion of the validity of the taxon is beyond the scope of this publication. The most recent diagnosis was provided by Müller (2002). The specimens from Miedary fit well with the description provided therein and share the characteristic features (overall proportions, biconcavity, and placement of the articular facets) with those of *Blezingeria*. While ZPAL V. 36/518 is nearly identical with described thoracic centra (Huene, 1951), ZPAL V. 36/517 possesses a feature unique among the known vertebral material assigned to *Blezingeria*—a distinct, flat, ventral edge. ZPAL V. 36/517 may represent a new caudal morphotype of *Blezingeria*, although the reported disparity might also be a result of intraspecific variation and/or erosion.

Order SAUROPTERYGIA Owen, 1860
Family NOTHOSAURIDAE Baur, 1889
Genus *NOTHOSAURUS* Münster, 1834
NOTHOSAURUS sp.
(Fig. 5A)

Material—A nearly complete cranium (ZPAL V. 36/200).

Stratigraphic Occurrence—M1–M2 layers (glauconite beds), M4.

Description—The specimen is 38 cm long, with its left side more complete and less deformed. The length from the tip of the snout to the anterior edges of the nares, orbits, and upper temporal fenestrae equals 84, 131, and 214 mm, respectively. The upper temporal fenestrae are 140 mm long anteroposteriorly. The cranium bears numerous cracks with the most severe being located in the central part of the specimen. The right premaxilla is missing its anteromedial portion while the left one is nearly complete, lacking only a small fragment at its tip. The orbits are located close to the nares, at a distance of 18 mm. The nares are tear-drop-shaped, tapering anteriorly. Both the frontals and parietals are fused. The palatal area is complete except for the damaged premaxillary part. The left orbital arch is broken just behind the orbit and is slightly displaced laterally. A subcircular pineal foramen is located at the posteriormost part of the skull table, anterior to parietal crest. Most of the teeth are missing, and those preserved are lacking their tips. The premaxilla had four main fangs and one smaller. The tooth row on the maxilla extends beyond the anterior margin of the upper temporal fenestra. The skull bones are fused.

Remarks—The presence of nothosaurs (Nothosauria indet.) was previously reported from Miedary on the basis of isolated postcranial bones from the dolomite beds (Sulej et al., 2011), which are also rich in microscopic teeth of eusauropterygians (Eusauropterygia indet., Pawlak et al., 2022). ZPAL V. 36/200 displays diagnostic features of *Nothosaurus* (after Rieppel, 2000), specifically the tooth row extending beyond the anterior margin of the upper temporal fenestra, paired maxillary fangs followed by smaller, more densely spaced, conical teeth, and a ratio of the longitudinal diameter of the upper temporal fenestra to orbit in the range of 2–4 (almost 3.6 in ZPAL V. 36/200).

ZPAL V. 36/200 differs from all other nothosaurs, except *N. cristatus*, *N. jagisteus*, and *N. edingerae* (Hinz et al., 2019; Rieppel, 2001a ; Rieppel & Wild, 1994), in having a sagittal crest posterior to the pineal foramen. The specimen differs from *N. cristatus* (Hinz et al., 2019) in the absence of the parietal crest anterior to the pineal foramen and in the more elongated external nares, and from *N. edingerae* (Rieppel & Wild, 1994) in having a subcircular pineal foramen, an anteriorly narrow upper temporal fenestra, and a relatively shorter nasal process of premaxilla. The pineal foramen appears to be located more posteriorly than in *N. jagisteus* (Rieppel, 2001a) although the morphology of that region shows some variability in other species of *Nothosaurus* and the diagnosis of *N. jagisteus* is mostly based on the cranial suture arrangement (Rieppel, 2001a), which is often not traceable in ZPAL V. 39/200. The number of fangs in each premaxilla (four large followed by one smaller) resembles that of *N. giganteus*, *N. yangjuanensis*, and *N. winkelhorsti* (Jiang et al., 2006; Klein & Albers, 2009; Rieppel & Wild, 1996). Due to the size differences, small sample, and fusion of skull sutures prohibiting identification of bone layout, we cannot determine whether ZPAL V. 36/200 is an ontogenetic variant of *N. edingerae*, *N. jagisteus*, or belongs to any other known species. Other *Nothosaurus* specimens from Miedary, including additional cranial material, are still under preparation. They are abundant (over 130 specimens) in bone-bearing units at the Miedary site.

Infraclass ARCHOSAUROMORPHA Huene, 1946
Order INCERTAE SEDIS
Family INCERTAE SEDIS
(Fig. 6C)

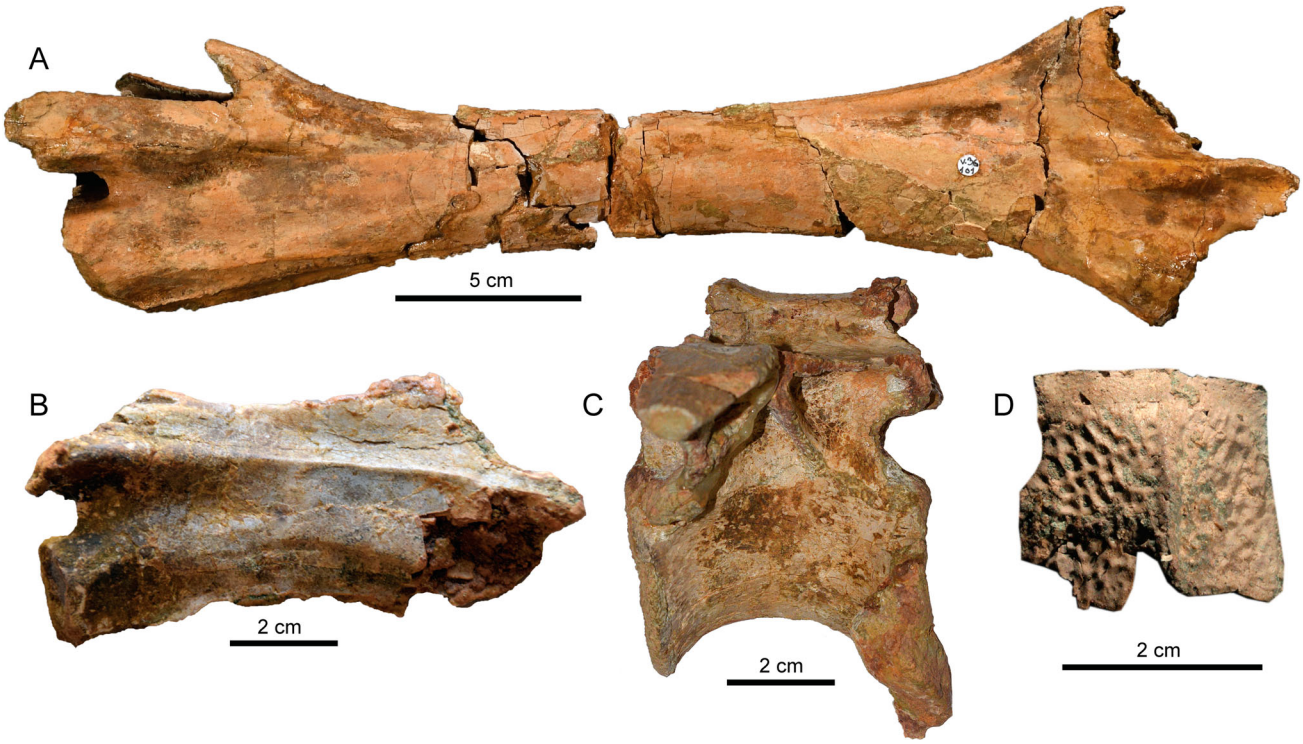

FIGURE 6. Archosauromorph remains from the Middle Triassic (Ladinian) of Miedary, Poland. **A**, tanystropheid *Tanystropheus* sp. ZPAL V. 36/101, middle cervical vertebra in right lateral view; **B**, Tanystropheidae indet. ZPAL V. 36/550, isolated vertebra in right lateral view; **C**, enigmatic armored archosauromorph ZPAL V. 36/400, vertebra in left lateral view; **D**, doswelliid *Jaxtasuchus* sp. ZPAL V. 36/582, dorsal paramedian osteoderm in dorsal view.

Material—ZPAL V. 36/400, series of associated cervical and dorsal vertebrae with osteoderms.

Stratigraphic Occurrence—M3 layer.

Description—The centra of the cervical vertebrae are elongated, being longer than those of the middorsal vertebrae. The centra are not pierced by a notochordal canal and the neural arches are fused to them, a condition that seems to be an apomorphic feature for the Archosauromorpha (Ezcurra, 2016). Ventrally, there is a single keel, the ventral extent of which does not reach beyond the centrum rims. Hypapophyses and epipophyses are absent. The diapophyses are connected to the centrum by four laminae. The prezygodiapophyseal and postzygodiapophyseal laminae, connecting the diapophysis with the lateral surface of prezygapophysis and the postzygapophysis, respectively, are present in ZPAL V. 36/400. The neural spines in ZPAL V. 36/400 are extremely low, saddle-shaped in lateral view, being placed close to the postzygapophyses. There is no trace of a spine table (i.e., the lateral expansion of the distal portion of the neural spine).

Remarks—Elongated cervical centra, being longer than those of the middorsal vertebrae, are present in archosauromorphs such as Tanystropheidae, in non-archosaurian archosauriforms such as *Vancleavea campi* Long & Murry, 1995, *Litorosuchus somnii* Li et al., 2016, and Doswelliidae (*Jaxtasuchus salomoni* Schoch & Sues, 2014, *Doswellia kaltenbachi* Weems, 1980), and, among archosaurs, in Poposauroidea and Dinosauromorpha (Ezcurra, 2016; Li et al., 2016; Nesbitt, 2011; Nesbitt et al., 2009). Low cervical vertebrae neural spines are present in some other archosauromorphs, including "protorosaurs" (e.g., Tanystropheidae), allokotosaurians (*Pamelaria dolichotrachela* Sen, 2003 and *Azendohsaurus madagaskarensis* Flynn et al., 2010), doswelliids (*Jaxtasuchus salomoni*, *Doswellia kaltenbachi*) and some dinosauromorphs (Ezcurra, 2016).

Several different types of osteoderms are preserved in association with ZPAL V. 36/400, making it similar to the archosauriforms *Litorosuchus*, *Vancleavea*, and doswelliids (Desojo et al., 2011; Li et al., 2016). In contrast to, for example, *V. campi* and *Jaxtasuchus salomoni* (SMNS 91083; Nesbitt, 2011; Nesbitt et al., 2009; Schoch & Sues, 2014), the single ventral keel of the vertebral centrum does not extend ventrally to the centrum rims in ZPAL V. 36/400. The prezygodiapophyseal and postzygodiapophyseal laminae are present in our specimen, in contrast to non-archosauromorph diapsids including doswelliids and *Vancleavea campi* (Ezcurra, 2016). Li et al. (2016) suggested the presence of such laminae in *Litorosuchus somnii.* The presence of four laminae connecting the diapophyses to the centrum is similar to what is also observed in some pseudosuchians (e.g., poposauroids *Effigia okeeffeae* Nesbitt & Norell, 2006, *Poposaurus gracilis* Mehl, 1915, and some Loricata; see Nesbitt, 2007). A detailed description of this animal will be provided in a separate paper.

Family TANYSTROPHEIDAE Camp, 1945
Genus *TANYSTROPHEUS* Meyer, 1852
TANYSTROPHEUS sp.
(Fig. 6A)

Material—Mostly complete middle cervical vertebra described herein (ZPAL V. 36/101), as well as over 500 other bones and teeth, including vertebrae from all of the axial column regions, ribs, femora, humeri, scapulae, coracoids, as well as cranial and pelvic elements.

Stratigraphic Occurrence—M1–M2 layers (glauconite beds), M4.

Description—The vertebra is relatively well preserved, although some of its parts can be observed on one side only—

the left prezygapophysis and the left postzygapophysis are missing, as is the ventral part of the posterior edge of the centrum. The specimen is 33 cm long (measuring from the ventralmost points of the anterior and posterior edges of the centrum) and 7 cm tall. The neural spine is nearly completely reduced near the midpoint of its anteroposterior length. The posterior part of the neural spine is posterodorsally inclined at an angle of 45° and the anterior part of the neural spine is inclined anterodorsally. The neural spine is hollow inside; its anterior and posterior margins are bifurcated and connect only at their respective dorsalmost extents, thus creating large elliptical foramina separated from the neural canal with a very thin bone layer (horizontallamelle sensu Wild, 1973). The right postzygapophysis is surmounted by a large epipophysis. The distance between the anterior tip of the right prezygapophysis and the posterior tip of the right epipophysis is 37.5 cm. The minimum height of the centrum is 40 mm. Its posterior and anterior articular surfaces are amphicoelous but not notochordal. The centrum has distinct lateroventral margins (sensu Nosotti, 2007). A well visible ventral keel runs through nearly the entire length of the centrum, although it is locally damaged. A small foramen (foramen vena vertebralis sensu Wild, 1973), 4 mm long and 2 mm wide, is located near the midpoint of the ventral side of the centrum.

Remarks—The vertebra ZPAL V. 36/101 displays a morphology characteristic for the mid-cervicals of *Tanystropheus*, especially the seventh vertebra (following the numbering system of Wild, 1973). From among the published material, it most closely resembles an unnumbered vertebra from the private collection of F. Martin, which was illustrated by Wild (1973: fig. 43, currently being transferred to SMNS) and attributed by him to *T. "conspicuus"*. The vertebral centrum is more than 2.5 times longer than its minimum height and the neural spine is very low. These features are considered diagnostic for mid-cervical vertebrae of *Tanystropheus* in the most recent taxonomic revision of the genus (Spiekman & Scheyer, 2019). Previously, only a handful of specimens from Poland have been unambiguously assigned to *Tanystropheus*—in the original description of the genus, Meyer (1847–1855) has mentioned a number of cervicals from the uppermost Muschelkalk of Laryszów, a village located only about 1 km away from the Miedary site (for more details see Skawiński et al., 2017). One additional specimen from the same site was illustrated by Langenhan (1903). Many more isolated bones from the Germanic Basin are known from the Upper Muschelkalk and Lower Keuper deposits of Germany and France (Spiekman & Scheyer, 2019). Most of these remains have been previously assigned to *Tanystropheus "conspicuus"* (Huene, 1907–1908, 1931; Wild, 1973), which was recently regarded as a *nomen dubium* by Spiekman & Scheyer (2019). The *Tanystropheus* material from Miedary is indistinguishable from *Tanystropheus "conspicuus*." Especially the cervicals bear a close resemblance in shape and size to the vertebrae described from several Ladinian (and possibly late Anisian) sites by Meyer (1847–1855), Huene (1902, 1907–1908, 1931), Edinger (1924), Peyer (1931), Adam (1953), Wild (1973), and Spiekman & Scheyer (2019). Some differences in the shape of neural spine and zygapophyses proportions can be noted between the specimens (A. R. pers. obs.), but these were already observed by Wild (1973) and could be the result of intraspecific variation or diagenetic deformation.

Both the cervicals from Miedary and those assigned to *T. "conspicuus"* differ in their morphology from those described from outside of the Germanic Basin—the neural spine is significantly taller in the former ones (A. R. pers. obs.). The three-dimensional preservation of the elements from Poland allows for a detailed osteological comparison with the second largest collection of isolated remains of *Tanystropheus* (around 230 specimens), recovered from the north-eastern Italy (Dalla Vecchia, 2006; Dalla Vecchia & Simonetto, 2018). Any further taxonomic interpretation is difficult without analyzing the rest of the fossil material from Miedary, which is currently undergoing preparation.

TANYSTROPHEIDAE indet.
(Fig. 6B)

Material—Mostly complete cervical vertebra, ?axis (ZPAL V. 36/550).

Stratigraphic Occurrence—M2 layer.

Description—The specimen has been laterally flattened due to compaction, but is still fairly three-dimensionally preserved. It is 26 mm tall at the lowest point and around 33 mm tall in the two highest points of the neural spine. The vertebra is elongate, with the centrum being originally about 2.5 times longer than its minimal height, although the exact centrum length cannot be obtained due to the incomplete preservation of its anteroventral portion. On the ventral side of the centrum, a pronounced keel is present. The left postzygapophysis is missing. The distance between the anterior tip of the right prezygapophysis and the posterior tip of the right postzygapophysis is 79 mm. The neural spine is probably preserved virtually intact and is relatively low. Its dorsal margin is concave, forming a nearly symmetrical curve, with the lowest point located near the midpoint of the anteroposterior length of the vertebra. The anterior margin of the spinous process is posterodorsally inclined and bifurcated, creating a concavity. The posterior part of the neural spine is not fully visible, but a relatively long and delicate process is present above a bony shelf located between the postzygapophyses (transpostzygapophyseal lamina sensu Spiekman et al., 2021).

Remarks—The only described tanystropheid known from the Ladinian sediments of Poland is *Tanystropheus* (Langenhan, 1903; Meyer, 1847–1855; Skawiński et al., 2017; Spiekman & Scheyer, 2019). The specimen ZPAL V. 36/550 corresponds to cervical vertebrae of *Tanystropheus* in morphology, yet some significant differences exist. The overall proportions of the vertebra do not resemble the most elongate *Tanystropheus* vertebrae, but rather the axis or the 11th cervical, which are relatively shorter. In the 11th cervical of *Tanystropheus* "*conspicuus*," the neural spine is dorsoventrally convex, not concave (A. R. pers. obs. 2023). While the morphology of the axis in *Tanystropheus hydroides* and *Tanystropheus longobardicus* is well known, at least laterally, no axis of *T.* "*conspicuus*" has ever been described, which is important, when taking into consideration the significant disparity of the neural spine morphology between these taxa. Only one, unpublished axis from the Upper Muschelkalk of Germany (SMNS 50226) is available for comparisons. Unfortunately, some of its features, especially the neural spine, have been reconstructed, making them difficult to assess. SMNS 50226 and ZPAL V. 36/550 differ in at least three characteristics: the relative length of prezygapophyses (much longer in ZPAL V. 36/550), the relative length of postzygapophyses and epipophyses (much longer in SMNS 50226) and the shape of the neural spine (lack of the pronounced anterior overhang in ZPAL V. 36/550). With the material recovered to date, all these differences preclude certain identification of the specimen ZPAL V. 36/550 as a *Tanystropheus* cervical, but further specimens undergoing preparation might help to resolve this matter.

In general proportions and morphology, the specimen most closely resembles the axes of tanystropheids, especially those of *Tanystropheus* spp. and an unnamed tanystropheid taxon described from the Moenkopi Formation (Arizona, U.S.A.) by Formoso et al. (2019); however, they exhibit a neural spine shape different from that of ZPAL V. 36/550. It is thus worth noting, that the specimen from Miedary exhibits a combination of morphological characters specific for various tanystropheid genera, and thus it cannot be readily assigned to any of them.

It may represent a new species, if the preserved anatomical details are not an effect of post-mortem alterations, but more material has to be recovered to reveal its phylogenetic relationships. Herein, we assign ZPAL V. 36/550 to Tanystropheidae indet.

Unranked ARCHOSAURIFORMES Gauthier, 1986
Family DOSWELLIIDAE Weems, 1980 sensu Desojo et al., 2011
Genus *JAXTASUCHUS* Schoch & Sues, 2014
JAXTASUCHUS sp.
(Fig. 6D)

Material—ZPAL V. 36/582, a nearly complete isolated dorsal paramedian osteoderm.

Stratigraphic Occurrence—M2 layer.

Description—The specimen is a relatively thin osteoderm with a smooth anterior lamina that is an articular surface for the anteriorly overlapping plate, as in doswelliids and aetosaurs (Desojo et al., 2011; Schoch & Sues, 2014). Although the posteriormost margin is not preserved, the bone is distinctively wider posteriorly, giving the osteoderm a trapezoid outline in dorsal view. The dorsal eminence takes the form of a longitudinal (anteroposterior), transversely compressed keel. It is slightly displaced from the midline of the osteoderm and divides the bone into two parts. In posterior view, both sides of the bone form an angle of 140°. One part is transversely wider than the other (respectively, 14 mm and 11 mm wide, measured along the osteoderm midline). The dorsal ornamentation consists of dense pits and is very similar to that on the posterior dorsal paramedian osteoderms of *Jaxtasuchus salomoni* (e.g., SMNS 90531; Schoch & Sues, 2014). The pits are relatively deeper and more pronounced on one side of the specimen.

Remarks—ZPAL V. 36/582 differs from *Ankylosuchus chinlegroupensis* Lucas et al., 2013, osteoderms, which are relatively thick, covered by relatively big pits, and lack a dorsal keel (Lucas et al., 2013). The latter feature is also true for *Archeopelta arborensis* Desojo et al., 2011. Furthermore, ZPAL V. 36/582 differs from *Rugarhynchos sixmilensis* Wynd et al., 2019, in which the dorsal eminence is spike-like (Wynd et al., 2019). ZPAL V. 36/582 differs from all doswelliids except *Jaxtasuchus* in the somewhat radial arrangement of pits, in contrast to their more random distribution in other Doswelliidae.

Although the isolated osteoderm may not be sufficiently diagnostic to identify a particular doswelliid genus, given the similar geological age and geographic proximity, ZPAL V. 36/582 most likely represents *Jaxtasuchus*, which is known from the Lower Keuper of Germany. Although *Jaxtasuchus* is a relatively common component in the Erfurt Formation (Schoch & Sues, 2014), only one specimen collected to date from the Miedary Beds can be referred to this taxon.

ARCHOSAURIFORMES indet.
(Fig. 7)

Material—ZPAL V. 36/09/23, ZPAL V. 36/09/24, ZPAL V. 36/412/01, ZPAL V. 36/439/01, ZPAL V. 36/501, ZPAL V. 36/502, ZPAL V. 36/503, ZPAL V. 36/511, ZPAL V. 36/513, ZPAL V. 36/515, ZPAL V. 36/519, ZPAL V. 36/520, ZPAL V. 36/561, ZPAL V. 36/590, ZPAL V. 36/591, ZPAL. V. 36/1301, isolated teeth.

Stratigraphic Occurrence—M1–M2 layers (glauconite beds), M3.

Description—Eight morphotypes of the archosauriform teeth can be distinguished in our sample.

The most common is the morphotype 1, bicarinate ziphodont teeth with the labiolingually compressed crown. It is represented by several teeth in our collection (e.g., ZPAL V. 36/501, ZPAL V. 36/511, ZPAL V. 36/513, ZPAL V. 36/520, ZPAL V. 36/590, ZPAL V. 36/591; Fig. 7A). The crown height is within the range of 7.5 mm (in ZPAL V. 36/520) to 34 mm (ZPAL V. 36/501). The crown base ratio (sensu Hendrickx et al., 2015; ratio of the labiolingual width to the mesiodistal length) is within the range of 0.65–0.85 for most of the specimens. The serration is rectangular, with narrow interdenticular sulci, and there are usually 4–5.5 denticles per millimeter on distal carina and 5–6.5 denticles per millimeter on the mesial one. The denticle density is roughly similar in all specimens referred to that morphotype, seemingly being independent from the overall size. Both lingual and labial surfaces of the crown are smooth, without any longitudinal flutes and ridges. ZPAL V. 36/7 and ZPAL V. 36/8, described by Sulej et al. (2011) and collected from a different horizon of the Miedary site, also represent the morphotype 1.

The morphotype 2, represented by specimens ZPAL V. 36/519 (Fig. 7B) and ZPAL V. 36/1301, is very similar to the morphotype 1, but differs in the density of denticles. There are very small tooth crowns, 3.2–6.5 mm in preserved length. They have 8–8.5 and up to 14 denticles per millimeter on the distal and mesial carina, respectively. The denticles are rectangular but slightly pointed apically. The value of the crown base ratio is 0.49. Near the base of the tooth crown, the mesial carina is pronounced and lacks denticles.

The morphotype 3 is represented by ZPAL V. 36/439/01 (Fig. 7C). It is slenderer than morphotype 1. The preserved tooth crown is 4 mm long, labiolingually compressed, with dense serrations present on both carinae (10–10.5 to per millimeter). The denticles are more triangular and point more apically than those of morphotypes 1 and 2. The labial and lingual surfaces are smooth.

The morphotype 4 is represented by ZPAL V. 36/515 (Fig. 7E). It is a recurved tooth, 11 mm long, nearly oval in cross section (with the crown base ratio equal to 0.88). The serrations are rectangular, weakly developed near the apex only on the distal carina, most likely due to weathering of the specimen. The mesial carina is very weakly developed.

Several tooth specimens in our collection (ZPAL V. 36/412/01, ZPAL V. 36/502, ZPAL V. 36/503, ZPAL V. 36/561) have serrations limited to the distal carina. The state of preservation of this material suggests that the lack of denticles along the mesial carina is not caused by taphonomy. Among them, two specimens are referred to as the morphotype 5, labiolingually compressed, bicarinate teeth. It is represented by ZPAL V. 36/502 (Fig. 7F) and ZPAL V. 36/503, which are about 10 mm long, with the crown base ratio equal to 0.537 and 0.467, respectively. The mesial carina of all specimens lacks denticles, while the density of the denticles on the distal carina equals 6–7 per millimeter. In ZPAL V. 36/502 three ridges are clearly visible on the labial and lingual surfaces demarcating the longitudinal depression. In ZPAL V. 36/503 such ridges are less distinct; however, a medially placed longitudinal depression is present.

Only one specimen is here referred to the morphotype 6. ZPAL V. 36/561 (Fig. 7G) is strongly recurved distally. It is labiolingually compressed, and apparently has only the distal carina. The denticles are densely distributed along the distal carina (9.5 per millimeter), relatively triangular in shape and pointed slightly apically. Very narrow, shallow apicobasal grooves are visible on the labial surface, and near the base of the tooth there are subtle transverse wrinkles, somewhat similar to the transverse undulation observed in theropod dinosaurs (Hendrickx et al., 2015) and other archosauriforms.

The seventh morphotype is represented by ZPAL V. 36/412/01 (Fig. 7D), a very small (2.8 mm long), labiolingually compressed tooth crown. It is slightly bulbous at the base, with a pronounced mesial margin, but without a distinct carina. The distal denticles are very small.

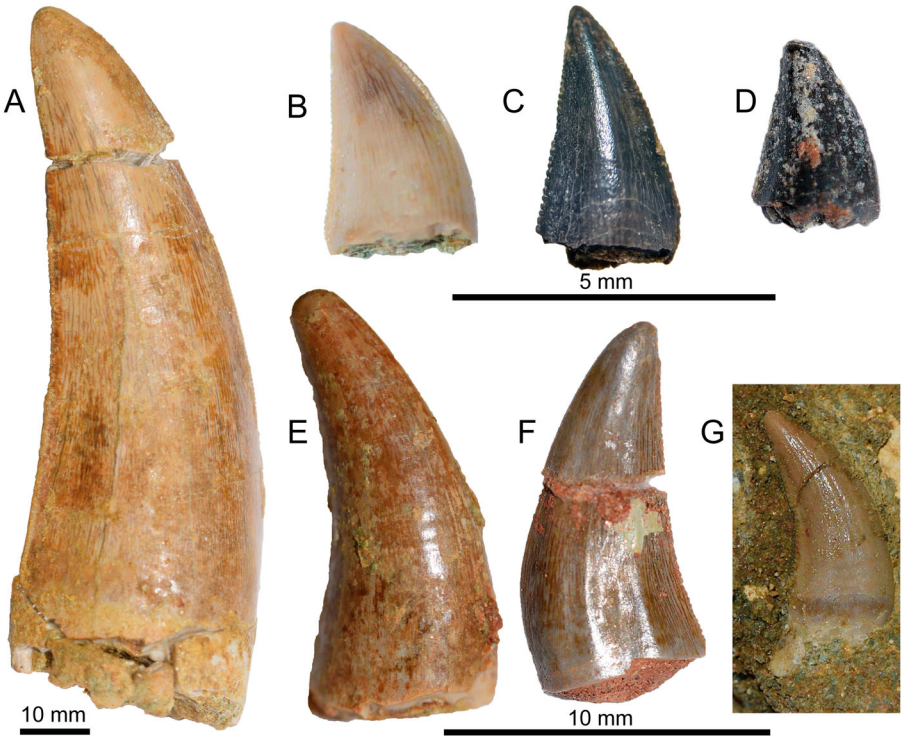

FIGURE 7. Archosauriformes indet., isolated teeth from the Middle Triassic (Ladinian) of Miedary, Poland. **A**, morphotype 1, ZPAL V. 36/501 in labial view; **B**, morphotype 2, ZPAL V. 36/519 in lingual view; **C**, morphotype 3, ZPAL V. 36/439/01 in labial view; **D**, morphotype 7, ZPAL V. 36/412/01 in ?labial view; **E**, morphotype 4, ZPAL V. 36/515 in lingual view; **F**, morphotype 5, ZPAL V. 36/502 in lingual view; **G**, morphotype 6, ZPAL V. 36/561 in labial view.

In addition to the material described here, Pawlak et al. (2022) reported two very small archosauromorph teeth collected from the same strata, ZPAL V. 36/09/23 and ZPAL V. 36/09/24. Although incompletely preserved, the former is similar to the morphotype 1 described here, while the latter is labiolingually flattened, and has triangular denticles that are pointing in the apical direction. Here it is referred to as the morphotype 8 (Pawlak et al., 2022:fig. 6B).

Remarks—The most common morphotype 1 resembles teeth type R1 from the Middle Triassic of Lower Keuper assigned by Schoch et al. (2018) to the carnivorous archosaur *Batrachotomus kupferzellensis* Gower, 1999. Such identification was already suggested for specimens ZPAL V. 36/7 and ZPAL V. 36/8 described from the Miedary site by Sulej et al. (2011), although coming from a horizon different from those described in this paper. However, they may represent the same taxon as the rest of the material referred here to that morphotype. As the unambiguous material of *Batrachotomus kupferzellensis* was not discovered in Miedary, we tentatively refer this morphotype to an indeterminate carnivorous archosauriform. The morphotypes 2 and 3 may represent the same, or closely related taxon.

The morphotype 4 resembles some phytosaur teeth; however, currently there are no recognized dental synapomorphies for that group (Stocker & Butler, 2013).

In overall morphology, morphotype 5 is similar to teeth of the archosauriform SMNS 96936 from the German Middle Triassic, briefly described as a morphotype R7 by Schoch et al. (2018). They share the recurved morphology, with bulbous base, and with the prominent parallel ridges on the labial surface. However, the teeth of SMNS 96936 are oval in cross section, with both carinae unserrated and limited solely to the apical region.

Serration limited to the distal carina only is a quite rare feature among archosauromorphs. This condition is present in the maxillary teeth of the proterosuchids *Proterosuchus fergusi* Broom, 1903, *P. goweri* Ezcurra & Butler, 2015, and "*Ankistrodon indicus*" (Ezcurra, 2016; Ezcurra & Butler, 2015; Modesto & Botha-Brink, 2008), the proterochampsid *Tropidosuchus romeri* Arcucci, 1990, and in some phytosaurs, such as *Nicrosaurus kapffi* (see Hungerbühler, 2000). Plausibly, such a condition may be present also in *Chanaresuchus bonapartei* Romer, 1971 and *Tasmaniosaurus triassicus* Camp & Banks, 1978 (see Ezcurra, 2014; Trotteyn & Ezcurra, 2020).

Given the morphology of the denticles of ZPAL V. 36/09/24 (morphotype 8) that are pointed and somewhat parallel to the longitudinal axis of the tooth, it is similar to the type R9 described by Schoch et al. (2018) and may belong to an herbivorous archosauriform.

DISCUSSION

We have recognized the presence of at least 24 species of fish, amphibians, and reptiles so far in the lower unit of the Miedary exposure. This number probably underestimates the actual diversity of the assemblage, since the described morphotypes of isolated teeth or scales likely represent multiple taxa. Moreover, the results of the rarefaction analysis (Fig. 8B) and comparisons with other assemblages of similar age from the Germanic Basin (Hagdorn et al., 2015; Schoch & Seegis, 2016; Schoch et al., 2018) suggest that this number is far from showing the actual biodiversity of the Miedary ecosystems.

The lower unit of the Miedary succession contains taxonomically diverse archosauromorph fossils (aside from tanystropheids). They are represented by a set of teeth, osteoderms referred to *Jaxtasuchus*, and fairly more complete remains of an enigmatic armored archosauromorph. The latter was not collected from the glauconite beds but from the overlying argillaceous mudstone bed (M3), which probably formed under more terrestrial conditions, but the largely featureless sediment hinders the interpretation of its origin. Noteworthy, no animal closely resembling the unidentified archosauromorph from

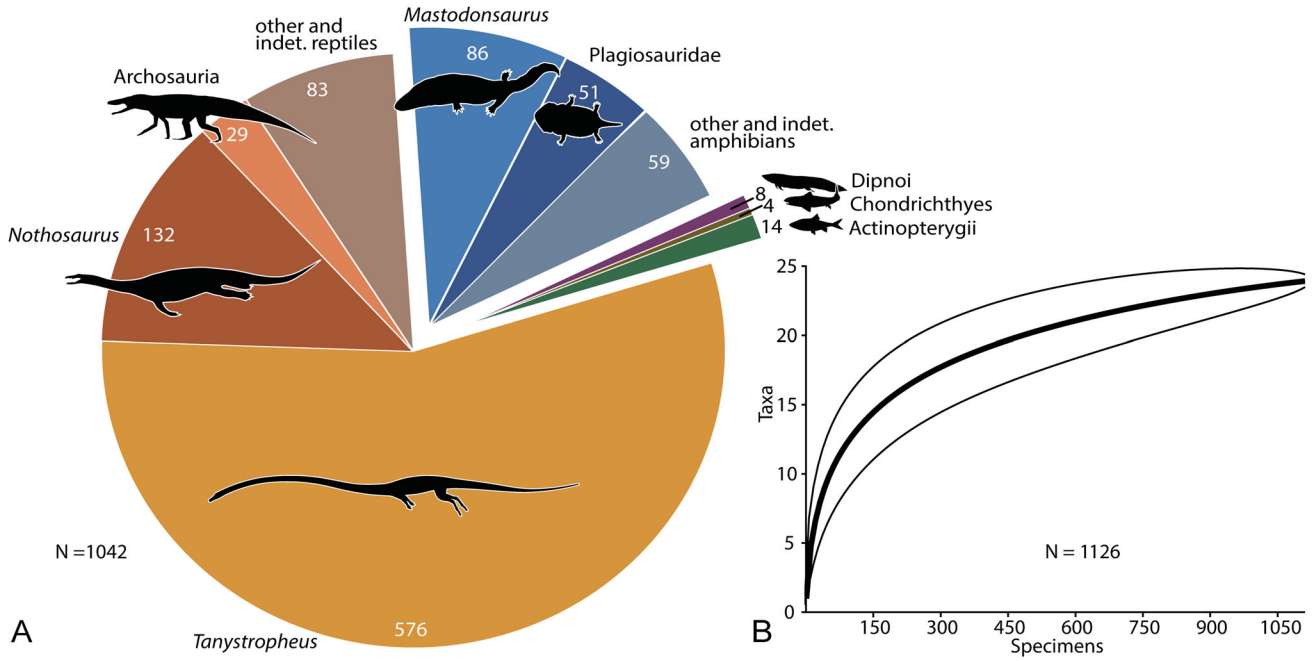

FIGURE 8. **A**, Taxonomic distribution of the vertebrate macrofossils (considered as specimens exceeding 1 cm in any dimension) in the glauconite beds (M1–M2) of the Miedary site; **B**, rarefaction curve for the sample of taxonomically identifiable vertebrate remains collected in the field from the M1–M4 beds of Miedary, Poland. Silhouettes are based on figures from Phylopic (*Batrachotomus* by S. Hartman) and Wikimedia Commons (*Nothosaurus* by N. Tamura, *Tanystropheus* by SlvrHwk, and *Gerrothorax* and *Paracyclotosaurus* by D. Bogdanov).

Miedary has been reported so far, neither from the Germanic Basin nor from elsewhere.

Marine Influence at the Miedary Site

The mixed composition of the assemblage from glauconite beds raises questions about the autochthonic origin of freshwater taxa. The occurrence of *Nothosaurus* and *Tanystropheus*, as well as the presence of glauconite and common carbonate cement, point to the direct connection of the site with a saline environment. Therefore, the co-occurring freshwater species may be regarded as adapted to saline conditions or transported, as well as coming from reworked freshwater facies. The occurrence of strictly freshwater conditions in Miedary seems improbable since there are no findings of taxa usually linked with freshwater conditions such as some temnospondyl amphibians (*Kupferzellia*, *Callistomordax*, and *Trematolestes*) or conchostracans. Also, the input of terrestrial taxa appears to be unusually scarce in contrast to freshwater deposits. Regarding the transportation scenario, we find no clear differences in the preservation mode of sauropterygians and temnospondyls, usually linked with marine and freshwater conditions, respectively. At this stage of the studies, animals connected with either environment appear to have similar origin and burial history. Their co-occurrence in the same environment can be explained by low salinity of the reservoir, tolerated by a limited number of freshwater organisms.

The lower salinity during the glauconite beds formation is supported by the set of marine taxa, which are less diverse when compared with fully marine deposits of the Upper Muschelkalk or the Monte San Giorgio area. The absence of ammonoids, brachiopods, conodonts, colobodontid actinopterygians, ichthyosaurs, and placodonts suggest conditions unfavorable for at least part of them due to intolerance of low salinities. A noteworthy exception are hybodonts, represented by several taxa in the glauconite beds assemblage. Besides their commonness, no specimens of *Hybodus plicatilis* and *Palaeobates* sp. were found, which are usually present in fully marine deposits (Pawlak et al., 2022). The interesting component of the assemblage is *Serrolepis suevicus*, known exclusively from the Germanic Basin, although its relatives are known from the Tethys area (see Griffith, 1977; Lombardo et al., 2008). The known record of *Serrolepis* shows its peculiar co-occurrence with mixed assemblages of sauropterygians and temnospondyls (Hagdorn & Mutter, 2011; Pawlak et al., 2022). If resulting from ecological preferences, the occurrence of *Serrolepis* can be regarded as indicative for low salinity conditions.

The assemblage from the glauconite beds was formed under complex conditions, involving numerous events of a post-depositional reworking as evidenced by features of the sediment. Nevertheless, we find limited arguments for mixing of remains from two separated aquatic ecosystems. On the basis of available data, the assemblage, including both sauropterygians and temnospondyls, existed in the marine nearshore zone with lowered salinity. In terms of salinity and taxonomic arrangement, the assemblage from glauconite beds is similar to that from the Albertibank or E4 layer of the Untere Graue Mergel in the western part of the basin (Hagdorn & Mutter, 2011; Hagdorn et al., 2015).

Marine Reptile Habitat

Tanystropheus fossils dominate in number over other tetrapod genera from the glauconite beds (Fig. 8A). So far we have recognized more than 500 isolated bones of this taxon in the identified material, more than from any other site reported to date. The lifestyle and use of the extremely elongated neck of *Tanystropheus* is a hotly debated topic among paleontologists (Beardmore & Furrer, 2018; Jaquier & Scheyer, 2017; Nosotti, 2007;

Renesto, 2005; Renesto & Saller, 2018; Rieppel et al., 2010; Spiekman & Scheyer, 2019; Spiekman et al., 2020a, 2020b, 2021). Remains of this genus are usually present in the coeval sites from the Germanic Basin, but so far have been reported only in relatively low quantities (Hagdorn, 1990; Hagdorn & Reif, 1988; Klein et al., 2022; Schoch, 2015; Schoch & Seegis, 2016; Schoch et al., 2022). An extensive review of the German collections has shown that around 250 isolated *Tanystropheus* bones and teeth can be identified (A. R. pers. obs.). These specimens were gathered during the last two centuries from over 60 sites, with only a few of them yielding more than 10 specimens. Thus, within the Germanic Basin, the Miedary locality can be regarded as the most productive source of *Tanystropheus* material to date. The unusual abundance of this peculiar reptile might suggest that the depositional setting of the glauconite beds is closely connected with the favored habitat of this animal. If this assumption is correct, it could help us better understand the biology of *Tanystropheus*. The current interpretation of the glauconite beds formation as formed in a brackish, restricted reservoir, relatively close to land, is consistent with previous studies on *Tanystropheus* suggesting an amphibious lifestyle related with a shoreline, rather than a fully aquatic and open-basinal mode of life (Beardmore & Furrer, 2018; Jaquier & Scheyer, 2017; Nosotti, 2007; Renesto & Saller, 2018; Spiekman et al., 2020a). This hypothesis is consistent with the general environmental conditions (shallow marine with a significant terrestrial input) present in the localities from the Aupa Valley, described by Dalla Vecchia (2006, 2010) and Dalla Vecchia & Simonetto (2018), in which *Tanystropheus* is also quantitatively dominant among the tetrapod finds.

Moreover, the observed variation among bones suggests the presence of at least one another tanystropheid in the Miedary glauconite beds. In the Middle Triassic, the co-occurrence of multiple tanystropheid taxa in one locality has already been reported from the Besano Formation, in the Monte San Giorgio area in Switzerland and Italy (Kuhn-Schnyder, 1974; Scheyer et al., 2020; Spiekman et al., 2020a), the Zhuganpo Member of the Falang Formation in China (Lu et al., 2018) and possibly the Gevanim and Saharonim formations of Makhtesh Ramon in Israel (Rieppel, 2001b). The Miedary site might represent a further case of this phenomenon, but contrary to the previous ones, related with a more nearshore and restricted environmental setting.

Cis-Uralian Affinities of the Miedary Fossil Assemblage

The Polish Middle Triassic strata are geographically intermediate between the outcrops located in southern Germany and the sites in Cis-Uralian Russia. In contrast to Miedary and other Germanic Basin localities, the well-recognized Cis-Uralian sites of similar age in Russia represent a continental interior with more terrestrial settings of deposition. Tetrapods usually linked with marine realms such as *Nothosaurus*, *Tanystropheus*, or *Blezingeria* are absent there. The components common with the Miedary site are temnospondyl amphibians and chroniosuchians. The chondrichthyan genera *Acrodus* and *Lissodus*, widely distributed in the marine and marginally-marine deposits of the Germanic Middle Triassic (Böttcher, 2015; Pawlak et al., 2022), were found in the Cis-Uralian region only in the Yarenskian Gorizont, which was influenced by a marine transgression (Minikh & Minikh, 1997; Tverdokhlebov et al., 2003). The actinopterygian *Serrolepis suevicus*, probably linked with brackish conditions (Hagdorn & Mutter, 2011; Pawlak et al., 2022), is absent in the Middle Triassic of the Cis-Uralian region.

While a significant part of differences between Miedary and southern Germany appears to result mainly from evolutionary changes, because the paleoenvironments in both areas were similar, the differences between Miedary and the Cis-Uralian region result from different depositional environments.

CONCLUSIONS

The Miedary locality preserves Lower Keuper deposits of early Ladinian age. It has so far yielded more than 1000 vertebrate remains and is still being actively excavated. Our preliminary observations suggest that the bone-rich glauconite beds found therein were formed under storm reworking. The overlying layers also bear vertebrate fossils, including an enigmatic armored archosauromorph, but their origin differs from the formation of glauconite beds. Fossils from the new site represent a diverse assemblage of fishes, amphibians, and reptiles, which points to the brackish conditions of the local environment. Most of these taxa were previously known from south-western localities of the Germanic Basin, which implies close biogeographic ties between Miedary and the rest of this area during the Ladinian. However, the exact determination of similarities between taxa from Miedary and the western part of the Basin must await completion of detailed osteological descriptions, which are currently in progress. A peculiar aspect of the new locality is the surprising abundance of *Tanystropheus*, which might be related to the habitat preference of this enigmatic reptile.

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AUTHOR CONTRIBUTIONS

ŁC, AR, WP, MT, and TSu led excavations at the Miedary site, which resulted in the collection of the described material. WP

and AR prepared the description of the geological section. ŁC and AR analyzed the numerical data. ŁC and WP prepared the figures. All authors collectively wrote and edited the manuscript.

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DISCLOSURE STATEMENT

No potential conflict of interest was declared by the author(s).

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