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Triassic fish faunas from Miedary (Upper Silesia, Poland) and their implications for understanding paleosalinity

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ABSTRACT

We describe two new fish-dominated faunas from the Middle Triassic (Ladinian) Miedary site, Upper Silesia, Poland, and present a comparative analysis of Middle-to-Late Triassic vertebrate assemblages from the Germanic Basin, in order to explore the influence of salinity on faunal composition. The composition of the assemblage from dolomite beds at Miedary is similar to those from the Muschalkalk facies, whereas the assemblage from glauconite beds appears to be the first brackish vertebrate assemblage of the *Serrolepis* lake-type recognized from the eastern Germanic Basin. Comparative analysis of all sites, using hierarchical clustering, nonmetric multidimensional scaling, and principal component approaches, revealed the existence of vertebrate taxa associated withfreshwater, brackish and marine conditions, as well as euryhaline taxa with wide salinity preferences. Moreover, it confirms the brackish nature of *Serrolepis*-bearing assemblages, and suggests that *Serrolepis suevicus* is a brackish specialist, indicative of oligohaline to miohaline paleosalinities. The Middle-Late Triassic vertebrate faunas appear dominated by stenohaline taxa, with a conspicuous separation of species living in the freshwater and marine conditions. The euryhaline taxa are rare, and comprise *Acrodus lateralis*, Eusauropterygia, *Lissodus nodosus*, and Saurichthyiformes.

1. Introduction

Fossils are often used for the reconstruction of paleoenvironments. In most cases, such inferences are based on either geochemical evidences or comparative analyses of composition of particular fossil assemblages (Martin, 2000; Armstrong and Brasier, 2005; Fischer et al., 2013). The geochemical analyses are less reliable for sediments exposed to diagenesis, which affects the primary composition of rocks and embedded fossils (Koch et al., 1992; Cochran et al., 2010; Fischer et al., 2013; Reynard and Balter, 2014).

The taxonomic analyses require a sufficient sample size and reference material. This is especially problematic in case of assemblages comprising completely extinct taxa or beds with a low fossil content (Ellison, 1951). Nonetheless, taxonomic analyses have potentially wider applications. In the present study, we discuss the significance of Triassic vertebrate microfossils for paleosalinity reconstructions. Findings are based on the comparative method applied to the assemblages from the Middle and Late Triassic of the Germanic Basin.

Assemblages belonging to the Lower Keuper strata (Middle Triassic, Ladinian) are of particular interest as subjects for comparative studies. The Lower Keuper records a rapid marine regression, being the final stage in the evolution of the Muschelkalk Sea (Franz et al., 2013). These deposits exhibit extraordinary horizontal and vertical variation in their lithology, reflecting the dynamically changing influences of marine and freshwater conditions, related to short-lived transgressive-regressive cycles (Hagdorn and Mutter, 2011; Franz et al., 2013). This lithological variability is reflected in the diversity of fossil vertebrate assemblages, especially well-recognized in the Franconia region (northern Baden-Württemberg, Germany) (Dorka, 2002; Hagdorn and Mutter, 2011; Hagdorn et al., 2015a, 2015b; Böttcher, 2015; Schoch and Seegis, 2016). The underlying Muschelkalk deposits are also locally rich in vertebrate remains (Liszkowski, 1973; Liszkowski, 1993; Hauschke and Wilde, 1999; Delsate and Duffin, 1999; Diedrich, 2003; Diedrich, 2009; Böttcher, 2015). They represent relatively stable euhaline or polyhaline environments (Korte et al., 2003; Franz et al., 2015), and are therefore a source of useful comparative material. The Lower Keuper yields material of particular value for research on the salinity preferences of fossil vertebrates, the main topic dealt with in this paper. We also describe two

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new vertebrate assemblages from the Lower Keuper outcrop in Miedary (Upper Silesia, Poland), containing numerous fish remains, accompanied by larger bones of amphibians, sauropterygians, and archosauromorphs (Sulej et al., 2011).

2. Geological setting

2.1. Description of sedimentary succession

The studied strata crop out in the abandoned claypit located between Miedary and Laryszów villages in southern Poland (N 50.4536, E 18.7702; Fig. 1A-B). The exposed succession (Fig. 2A) is about 5 m thick and is composed of three lithologically different units. The lower and upper units contain horizons especially rich in vertebrate remains (bonebeds), and both are well exposed. On the other hand, no vertebrate fossil have been found in the middle unit (about 250 cm thick), which is poorly exposed and has been only cursorily described.

The lower unit is composed of siliciclastic rocks. The exposed succession starts with a 10 cm thick layer of poorly sorted green sandstone, overlying poorly exposed reddish mudstone. This sandstone is predominantly strongly lithified, and contains shells of bivalves tentatively identified as *Unionites* sp., numerous small bones, and mica grains. It is overlain by an approximately 120-cm thick layer of reddish to greenish, calcareous, and strongly bioturbated mudstone, containing numerous root traces, and irregular grey-colored zones. Several interbeds of green, fine-grained sandstone occur in the lower part of this layer. They are up to 10 cm thick and have erosional lower contacts. The internal structure of some interbeds comprise sets of roughly parallel, undulating laminae. The sets within a single interbed are separated by erosional surfaces. Both the internal and basal erosional surfaces of the interbeds form gentle curvatures. Due to a weak lithification of the rock, details of the interbed laminations are hard to determine, although the observed features resemble hummocky cross-stratification. Within the lower unit, a discontinuity has been recognized, above which the red mudstones continue but contain more roots traces, and horizontal grey-colored zones.

The middle part of the succession consists of grey to bluish clay. It lies in a sedimentary continuity with the red mudstone. Only the lowermost and the highest parts of this unit are exposed on the surface. Manual drilling allowed us to estimate the thickness of this interval (c.a. 250 cm). The lowermost part of the clays contains minute gypsum crystals, and plant debris.

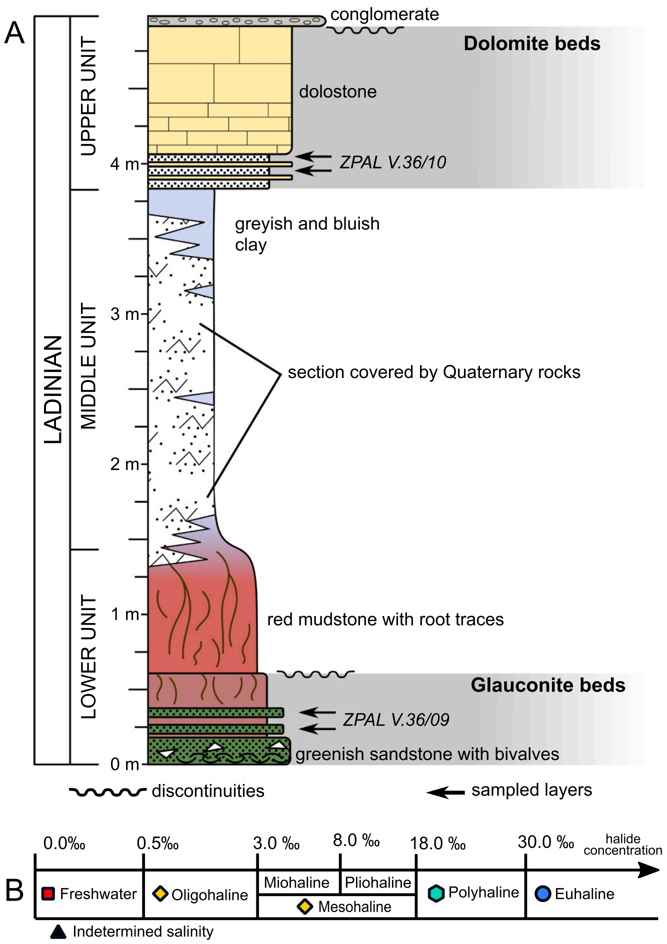

Fig. 2. Geological section of the Miedary outcrop (A) and explanation of the salinity categories used in the text (B), after Remane and Schlieper (1972). Symbols next to the salinity ranges are applied in the Fig. 8. Diamonds reflects all salinities from oligo to the pliohaline.

Sandstones and carbonates dominate in the upper part of the section. The underlying clay package ends with a 15-cm-thick layer of loosely lithified calcareous sandstone. It is overlaid by a conspicuously bedded

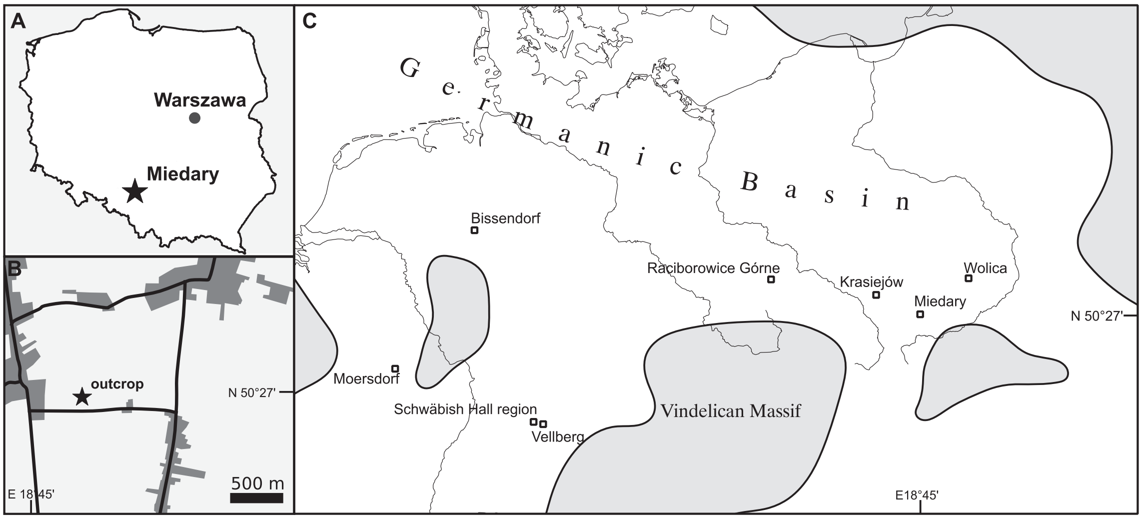

Fig. 1. Geographical setting of the studied localities. A. Miedary locality on the contour map of Poland. B. Detailed location of the studied outcrop. C. Map of paleontological sites included into the comparative faunal analysis on contour maps of the Germanic Basin (borders of the massifs for the early Ladinian period, after Franz et al., 2015).

100 cm package of the yellowish sandy dolostone. In the lower part, the beds are relatively thin (c.a. 5 cm) and contain several interbeds of a white, loosely lithified sandstone. The interbeds have sharp, irregular lower boundaries, and do not exhibit internal lamination. In the upper part of the unit, the dolostone beds are thick (c.a. 30 cm) and contain rare, poorly preserved bivalves. The carbonates are overlain by a thin layer of the coarse conglomerate.

The features described above allow a preliminary paleoenvironmental interpretation of the lower and upper unit. A high contribution of the quartz and mica grains in the sandstones and mudstones of the lower unit suggest near-shore conditions, with a high input of terrigenous material. They are accompanied by the green grains resembling glauconite, suggesting a shallow marine setting. The interbeds of green sandstones most probably represent high-energy events. If the proposed interpretation of these interbeds as being hummocky-cross stratified is accurate, they were deposited at a depth of 30–50 m, between fair-weather and storm wave bases. Above the discontinuity, the lower unit mudstones are massive, rich in root traces and grey-colored zones suggesting the persistence of pedogenic processes. The dominance of carbonate sedimentation in the upper unit, with a considerably lower input of quartz grains compared to the lower unit, suggest formation in a more distal marine environment. This interpretation is supported by the sandy interbeds, which probably represent distal tempestites, formed below the storm wave base.

2.2. Paleontology

Ganoid scales, teeth, and isolated bones occur across the lower and upper units. However, they are clearly concentrated within interbeds of green sandstone in the lower unit, and interbeds of the white sandstone in the upper unit. As we reasoned above, both kinds of inserts probably reflect high-energy events. The intervals containing these interbeds are referred to in this paper as the glauconite and dolomite beds, respectively. Fossils within the condensed facies would originate from reworking of the former sediment under the storm conditions, as proposed in the bonebed formation model of Reif (1982). The general setting of the Miedary locality was outlined by Sulej et al. (2011). They reported the occurrence of *Nothosaurus* bones, ganoid scales, and *Palaeobates* teeth from the dolomite beds. Within the glauconite beds, bones of nothosaurs have been recognized as well, together with temnospondyls, tanystropheids, and other archosauromorphs (Sulej et al., 2017). Vertebrates were previously reported from the Lower Keuper deposits in Upper Silesia. Eck (1863) and Assmann (1914, 1937) reported occurrences of *Gyrolepis*, *Saurichthys*, and *Hybodus* in the Miedary Beds, whereas Siewniak-Madej (1982) reported only undetermined fish and reptiles bones. The spatiotemporally close to Miedary are well-recognized localities in Franconia, known for exceptional finds of temnospondyls, archosaurs, and lungfish (e.g., Schultze, 1981; Schoch, 1997; Gower, 1999; Hauschke and Wilde, 1999).

2.3. Stratigraphy

The section studied exposes the Miedary beds, an informal stratigraphic unit of the Silesian Triassic (Kotlicki, 1974). They are regarded as a lithostratigraphic equivalent of the Sulechowice Beds in the central Poland, the Coalclay Beds in the Holy Cross Mountains region, and the Erfurt Formation in Germany (Gajewska, 1988; Szulc et al., 2015). The Miedary beds are composed of alternating clays, sandstones and carbonates, similar to the Erfurt Formation (Assmann, 1914; Siewniak-Madej, 1982; Franz et al., 2013). The latter were deposited in shallow, marginal marine, lagoonal, lacustrine, and fluvial environments (Franz et al., 2013; Nitsch, 2015), resulting in a scarcity of the biostratigraphically most informative Triassic index fossils, such as ceratites and conodonts (Franz et al., 2013; Hagdorn et al., 2015a, 2015b). Until now, no index fossils have been found in the Miedary beds, except for palynomorphs. The assemblage reported from the grey clays of Miedary (Sulej et al., 2011) is similar to those known from the regional subunits of the Lower Keuper (Siewniak-Madej, 1982; Orłowska-Zwolińska, 1983; Fijałkowska, 1992; Sulej et al., 2011). They represent the *dimorphus* zone, also represented from the uppermost Muschelkalk and Lower Keuper of the western part of the Germanic Basin and Alpine region (Orłowska-Zwolińska, 1983; Fijałkowska-Mader et al., 2015).

The palynostratigraphic zonation is of low resolution compared to marine faunal zonations, which would allow a more precise dating of the outcrop. Moreover, palynomorph assemblages probably reflect ecological rather than evolutionary changes (Franz et al., 2013). Ceratites and conodonts, which have been found in the Muschelkalk deposits underlying the Erfurt Formation, revealed the strongly diachronous nature of the boundary between the Muschelkalk and the Lower Keuper in the western part of the Germanic Basin (Franz et al., 2013). Fortunately, the Miedary locality is close to the Muschelkalk outcrop in the Laryszów village (Fig. 1B). Because both outcrops lie roughly along the strike line, the dip in this region is minimal, and tectonic discontinuities are rare, we assume that the layers exposed in Miedary are not markedly younger than those in Laryszów.

The Laryszów site section exposes the Boruszowice Beds (Szulc, 2007), directly underlying the Miedary beds in sedimentary continuity (Zawidzka, 1975). The Boruszowice Beds belong to the *spinosus* ammonoid zone (Salamon et al., 2003) and *haslachensis* conodont zone (Zawidzka, 1975), both correlated with the early Fassanian (Franz et al., 2013). They are the uppermost biozones of the Muschelkalk in Upper Silesia, whereas in Southern Germany they are followed by several younger zones (Salamon et al., 2003; Franz et al., 2013). Regarding the strongly diachronous boundary between the Muschelkalk and Lower Keuper, this implies that the early Fassanian is the oldest possible age for the Miedary outcrop. A slightly different hypothesis was proposed by Szulc (2000), who inferred a Longobardian age for the Lower Keuper deposits in the eastern Germanic Basin. He correlated the Anisian/Ladinian boundary with the Trochitenkalk Formation (*flexuosus* ammonoid zone), and late Fassanian with Boruszowice Beds (*spinosus* ammonoid zone). On the other hand, the magnetostratigraphic study of Nawrocki and Szulc (2000) correlated the Boruszowice Beds with the early Fassanian, implying a similar age for the beginning of the Lower Keuper deposition. Another magnetostratigraphic study of the Triassic strata of the Polish Lowland and Upper Silesia (Nawrocki et al., 2015) has not yielded useful dates for the Lower Keuper, except the recognition that the Lower Keuper sediments are close to the Fassanian/Longobardian boundary. However, the polarity data were derived from a drill core located in the central part of the Basin, whereas the Miedary site is located marginally. Considering the possible time lapse between the deposition of beds cropping out in Laryszów and Miedary, and considering the more recent correlation of faunal zonations for the Germanic Basin (Brack and Rieber, 1993; Bachmann and Kozur, 2004; Franz et al., 2013, 2015) and magnetostratigraphic units (Nawrocki and Szulc, 2000), we consider the age of the Miedary outcrop as the middle to upper Fassanian.

3. Materials and methods

3.1. Fossils extraction and comparative material

The macrofossil remains were collected at Miedary between 2014 and 2020 and cleaned mechanically with pneumatic tools and needles. The microfossils were obtained from rock samples dissolved in 10% formic or acetic acid (in case of carbonates or strongly lithified siliciclastics, the acid used depended on the lithification level) or softened in hot water (in case of weakly lithified siliciclastics). After dissolution, the residues were wet sieved to remove clay particles. All phosphate microfossils were picked with aid of stereoscopic microscopes from the residues after complete drying. The exact position of the samples in the geological section is shown on Fig. 2A. The total weight of samples obtained from each bone-bed was more than 30 kg. To avoid bias resulting from local sampling, material was collected from different sites within the fossiliferous interval. In total, we identified 1283 specimens, including 1272 microfossils from washed samples, of which 517 came from the glauconite (sample ZPAL V.36/09) and 755 from the dolomite beds (sample ZPAL V.36/10). We collected 11 macrofossils from the weathered rock surface or from mechanical preparation (9 from the glauconite beds, and 2 from the dolomite). All specimens are housed in the collection of the Institute of Palaeobiology of the Polish Academy of Sciences (ZPAL). Comparative material investigated personally comprised several specimens of *Polyacrodus keuperianus* housed in the Staatliches Museum für Naturkunde in Stuttgart (SMNS), including SMNS 87104 and SMNS 56356. We also investigated several dozen fish scales and teeth from Laryszów and Krasiejów localities (unnumbered), housed in the historical collection of ZPAL. For descriptions of chondrichthyan remains, we followed the anatomical terminology of Bratvold et al. (2018).

3.2. *Vertebrate assemblages chosen for the comparative study*

We have selected twelve Muschelkalk and Keuper fossil assemblages for the comparative analysis, in addition to the two new assemblages from Miedary. We selected assemblages with the following characteristics: (1) they yielded phosphate microfossils or macro and microfossils, (2) their composition was not significantly influenced by taphonomic sorting, (3) their putative paleosalinities were known. The assemblages came from six areas within the Germanic Basin (Fig. 1C). Assemblages from Lehrbergbanks and Albertibank were collected at numerous sites, located mainly around the Schwäbish Hall in the northern Baden-Württemberg (Fig. 1C). The Vellberg site near Schwäbisch Hall provided three assemblages from different beds (E4, E5, E6; numeration in stratigraphic order after Schoch and Seegis, 2016). Two bonebeds were identified within the Krasiejów succession, but only the assemblage from the lower ‘lacustrine’ bed are included in the present study. The assemblages represent a timespan from the early Anisian (Bithynian) to the latest Carnian. Note that the age of strata exposed at Krasiejów is disputed; it is considered early Norian based on lithostratigraphy (Szulc and Racki, 2015; Szulc et al., 2015), but a late Carnian age is better supported biostratigraphically (Dzik and Sulej, 2007; Kozur and Weems, 2010; Lucas, 2015; Dzik and Sulej, 2016; Geyer and Kelber, 2018; Lucas, 2020).

Salinity categories used in this paper (Fig. 2B) follow Remane and Schlieper (1972). Data for temporal changes in salinity within the Muschelkalk Sea come from the geochemical studies of Korte et al. (2003) and Franz et al. (2015). They indicate euhaline salinity during the Lower Muschelkalk deposition, and euhaline decreasing to polyhaline during the deposition of the Upper Muschelkalk. Schoch and Seegis (2016) interpreted the fossiliferous horizons E4, E5, and E6 from Vellberg as mesohaline, miohaline, and oligohaline, respectively. Lehrberg beds were deposited within extensive freshwater lakes, with more saline water concentrated in their deepest, uninhabited portions (Seegis, 1997). Arguments for the freshwater nature of the Krasiejów lacustrine assemblage have been provided by Zatoń et al. (2005) and Bodzioch and Kowal-Linka (2012). At least partially saline conditions during the formation of Albertibank are supported by sediment features reportedby Hagdorn and Mutter (2011). The list of assemblages, their stratigraphic positions and putative paleosalinities are summerised with references in Table 1.

Table 1

Vertebrate assemblages chosen to comparative analysis, their stratigraphic positions and putative paleosalinities.

Assemblage name (paleontological description reference)	Chronostratigraphy[a]	putative paleosalinity[b]	References
Albertibank (Hagdorn and Mutter, 2011)	late Fassnian	oligohaline/ mesohaline	[a]Franz et al., 2013, [b]Hagdorn and Mutter, 2011
Bissendorf (Diedrich, 2009)	latest Anisian/ earliest Ladinian	polyhaline	[a]Diedrich, 2009, [b]Franz et al., 2015
Krasiejów Lower (Kowalski et al., 2019)	late Carnian	freshwater	[a]Geyer and Kelber, 2018; [a] Lucas, 2020, [b] Zatoń et al., 2005; [b]Bodzioch and Kowal-Linka, 2012
Lehrbergbank Lower (Seegis, 1997)	late Carnian	freshwater	[a,b] Seegis, 1997
Lehrbergbank Middle (Seegis, 1997)	late Carnian	freshwater	[a,b]Seegis, 1997
Lehrbergbank Upper (Seegis, 1997)	late Carnian	freshwater	[a,b]Seegis, 1997
Miedary Glauconite beds (herein study)	early/middle Fassanian	?	present study
Miedary Dolomite beds (herein study)	early/middle Fassanian	?	present study
Moersdorf (Delsate and Duffin, 1999)	latest Anisian/ earliest Ladinian	polyhaline	[a]Delsate and Duffin, 1999, [b] Franz et al., 2015
Raciborowice Dolne (Chrząstek, 2008)	Bithynian	euhaline	[a]Chrząstek, 2008, [b]Korte et al., 2003
Vellberg E4 (Schoch and Seegis, 2016)	late Fassanian/early Longobardian	mesohaline	[a]Franz et al., 2013, [b] Schoch and Seegis, 2016
Vellberg E5 (Schoch and Seegis, 2016)	late Fassanian/early Longobardian	miohaline	[a]Franz et al., 2013, [b]Schoch and Seegis, 2016
Vellberg E6 (Schoch and Seegis, 2016)	late Fassanian/early Longobardian	oligohaline	[a]Franz et al., 2013, [b]Schoch and Seegis, 2016
Wolica (Liszkowski, 1973)	Bithynian	euhaline	[a]Liszkowski, 1973; [a]Nawrocki and Szulc, 2000, [b]Korte et al., 2003

[a] Reference for chronostratigraphy.

[b] Reference for salinity setting

3.3. *Statistical analyses*

To estimate reliability of the samples from Miedary, we plotted rarefaction curves for both fossiliferous layers separately, using Past 3.23 software. To prepare graphic presentation of the taxa absolute abundances within the assemblages, we used R 4.0.3 software with ggcharts extension to ggplot2. For the comparative analysis, we prepared a presence/absence matrix of taxa occurring within the selected Middle-Late Triassic assemblages from the Germanic Basin (Supplementary Table S1). We used Cluster Analysis (CA) based on the UPGMA algorithm, and Non-metric Multidimensional Scaling (NMDS) to check similarity between assemblages, and Principal Component Analysis (PCA) to identify the taxa responsible for differences. CA and PCA analyses were performed in Past 3.23 software and NMDS analyses in R 4.1. The presence/absence matrix was based on slightly modified taxonomic data derived from the literature.

3.4. *Data taxonomic standardization*

The composition of the analyzed assemblages has been taken from Chrząstek (2008) for Raciborowice Górne, Liszkowski (1973) for Wolica, Diedrich (2009) for Bissendorf, Delsate and Duffin (1999) for Moersdorf, Hagdorn and Mutter (2011) for the Albertibank horizon in the Schwäbish Hall region (Franconia), Schoch and Seegis (2016) for the

Vellberg locality, Seegis (1997) for the Lehrbergbank horizons, and Kowalski et al. (2019) for Krasiejów. Taxonomic criteria applied and methods of fossils collecting were not consistent, making these literature data difficult to compare. Before coding of the presence/absence matrix, we evaluated the literature data to unify the classification methodology and remove redundancy. Scales with faint ornamentation reported from Raciborowice Górne and Bissendorf, described as Actinopterygii indet. (Chrząstek, 2008; Diedrich, 2009), are regarded here cf. Redfieldiiformes (Hagdorn and Mutter, 2011; Kowalski et al., 2019). The ridges-bearing scales from Lehrbergbanks, although close to *Turseodus* (see Seegis, 1997) are here we identified as cf. *Gyrolepis* because of lack of the differentiating characters between isolated scales of these genera. Among actinopterygians remains from Krasiejów, the scales allegedly belonging to semionotiforms (Kowalski et al., 2019), we recognize rather as cf. *Gyrolepis*, based on their ornament, shape, and peg and socket articulation. Semionotiforms have been reported from Wolica, Bissendorf and Krasiejów localities on the base of isolated molariform teeth (Liszkowski, 1973; Diedrich, 2009; Kowalski et al., 2019). Similar teeth have been identified also in Moersdorf (Delsate and Duffin, 1999). We regard this identification as doubtful because occurrence of similar teeth morphologies among bobastranids, perleidids or colobodontids, as emphasized also by Delsate and Duffin (1999). More convincing is the identification of Semionotiforms and their relatives (*Semionotus* sp., *Lepidotes* sp., Semionotidae indet.) from Lehrbergbanks because of findings of the jaw bones and characteristic dorsal scales (Seegis, 1997). Nevertheless, they are too fragmentary to determine their certain taxonomic position, and require reinvestigation in the light of the newest research on ginglymodian phylogeny and taxonomy. Therefore, we decided to classify all the above-mentioned isolated Semionotiform-like fossils as cf. Semionotiformes. To this category we decided to classify also Semionotiforms reported from the E5 horizon in Vellberg, due to lack of graphical documentation validating more precise identification. A similar case is *Dipteronotus* from the E5 and E6 horizons at Vellberg (Schoch and Seegis, 2016). This also lacks documentation, and may represent *Serrolepis suevicus* or another polzbergid genus. This seems consistent with the intraspecific variability of *S. suevicus* (Hagdorn and Mutter, 2011; Böttcher, 2015), as well as the reinterpretation of the late Middle Triassic occurrences of *Dipteronotus* as other polzbergids, such as *Serrolepis* or *Stoppania* (Lombardo et al., 2008; Hagdorn and Mutter, 2011). *Lissodus* and *Lonchidion* have a long history of taxonomical reshuffling (Rees and Underwood, 2002). *Lissodus* occurrences are reported from Palaeozoic deposits, whereas the oldest occurrence of *Lonchidion* was reported from the Middle Triassic of England (Patterson, 1966; Rees and Underwood, 2002). Minute crushing shark teeth from the Albertibank horizon, interpreted as *Lonchidion* by Hagdorn and Mutter (2011), differ significantly from those known in species of this genus, and fit rather those of *Lissodus*. On the other hand, the teeth reported from Lehrbergbanks as *Lissodus* (see Seegis, 1997) have features specific for *Lonchidion*: strongly pronounced occlusal crest, subtle ornament, and parallel-sided labial peg (Rees and Underwood, 2002). The Lower Keuper is known for the relatively frequent occurrences of coelacanths (Hagdorn and Mutter, 2011; Schoch and Seegis, 2016). which are present also at Krasiejów, whereas their remains from Albertibank or Vellberg are difficult to identify (Hagdorn and Mutter, 2011; Schoch and Seegis, 2016) and are not included in the analysis.

4. Results

4.1. Fish assemblages from Miedary

The taxonomic compositions of the two new assemblages from Miedary require brief descriptions in order to validate the results of the analyses and justify coding of the dataset. Descriptions are based mainly on microfossils collected from the dissolved bulk samples, but also several macro specimens are included. Both assemblages contain at least ten separate fish species belonging to hybodont sharks, 'palaeopterygian' actinopterygians and neopterygians. Additionally, one species of sarcopterygian occurs in the assemblage grom the glauconite beds.

4.1.1. Glauconite beds

Polyacrodus keuperianus (Winkler, 1880).

Material: 25 isolated teeth (numbered specimens: ZPAL V.36/09/05, ZPAL V.36/09/06; Fig. 3A1,2; B1,2).

Remarks: Most of the teeth preserved only one cusp, either central or lateral, except for two specimens with preserved two cusps. Therefore, they were most likely to be primary tricuspid. Cusps are ornamented by loosely arranged apicobasal ridges along their entire height, and roughly round in cross-section. Furrows between cusps are deep.

The morphology of these specimens is consistent with *P. keuperianus* teeth reported by Dorka (2003) and SMNS 96417 from the Lower Keuper of Germany.

Polyacrodus cf. *polycyphus* Agassiz, 1843.

Material: One tooth (ZPAL V.36/604; Fig. 4A1, A2, A3).

Remarks: The assignment of this relatively big hybodont tooth is tentative. Only one arm of the tooth is preserved. It bears four cusps, each ornamented by several apicobasal ridges. The tooth is high-crowned with shallow furrows between the cusps. The root has minute pores and overall is slightly higher than the crown. We decide not to include this species into the taxonomic comparison of assemblages, because of its incompleteness and doubtful identification.

Acrodus cf. *lateralis* Agassiz, 1839.

Material: Three teeth (numbered specimens: ZPAL V.36/09/02, ZPAL V.36/09/03; Fig. 3C1–2, D).

Remarks: The teeth are ornamented with subtle apicobasal ridges, bifurcating close to the edges of the teeth. On the occlusal surface, the mesiodistal crest is present, running across the teeth. Two morphotypes have been recognized in the assemblage from glauconite beds: morphotype 1 is represented by flat, loaf-shaped teeth (ZPAL V.36/09/02, Fig. 3D), whereas morphotype 2 is represented by one specimen (ZPAL V.36/09/03, Fig. 3C1–2) with preserved root, relatively short mesiodistal length, strongly convex occlusal surface, and lacking apicobasal ridges.

Lissodus nodosus Seilacher, 1943.

Material: Eight teeth (numbered specimen: ZPAL V.36/09/04, Fig. 3E1, 2).

Remarks: Teeth are minute, straight or slightly curved in occlusal view. The crown is low, merged, massive, with conspicuous central cusp, and non-erected lateral-most portions of arms. Contact between root and crown is incised. The occlusal crest is variously developed, from poorly visible to conspicuous.

Hybodontiformes indet.

Material: Three placoidal scales (numbered specimen: ZPAL V.36/09/09, Fig. 3F-1) and one fragment of fin spine.

Remarks: The scales represent hybodontid-type morphology. They have a conspicuous neck, and the robust flat crown is twisted caudally. The bone parts interpreted as fin spine fragments are covered by loosely arranged tubercles covered by enameloid.

cf. *Gyrolepis* Agassiz, 1935.

Material: 302 scales (numbered specimen: ZPAL V.36/09/12; Fig. 3H1–2), and 43 teeth (numbered specimen: ZPAL V.36/09/11; Fig. 3G).

Remarks: Ganoid scales with longitudinal ridges, smooth edges and conical teeth with fusiform ornament dominate the assemblage from glauconite beds. Scales and teeth with this morphology are commonly classified as *Gyrolepis* sp. (see: von Meyer, 1849; Liszkowski, 1973; Duffin and Gaździcki, 1977; Delsate and Duffin, 1999; Böttcher, 2015; Korneisel et al., 2015; Nordén et al., 2015). However, other Late Triassic genera with a similar scalation are known from the Newark (Schaeffer, 1952) and the Bermejo Basins (Lopez-Arbarello et al., 2006). Thus, we are caution in unambiguously referring isolated microfossils to *Gyrolepis*.

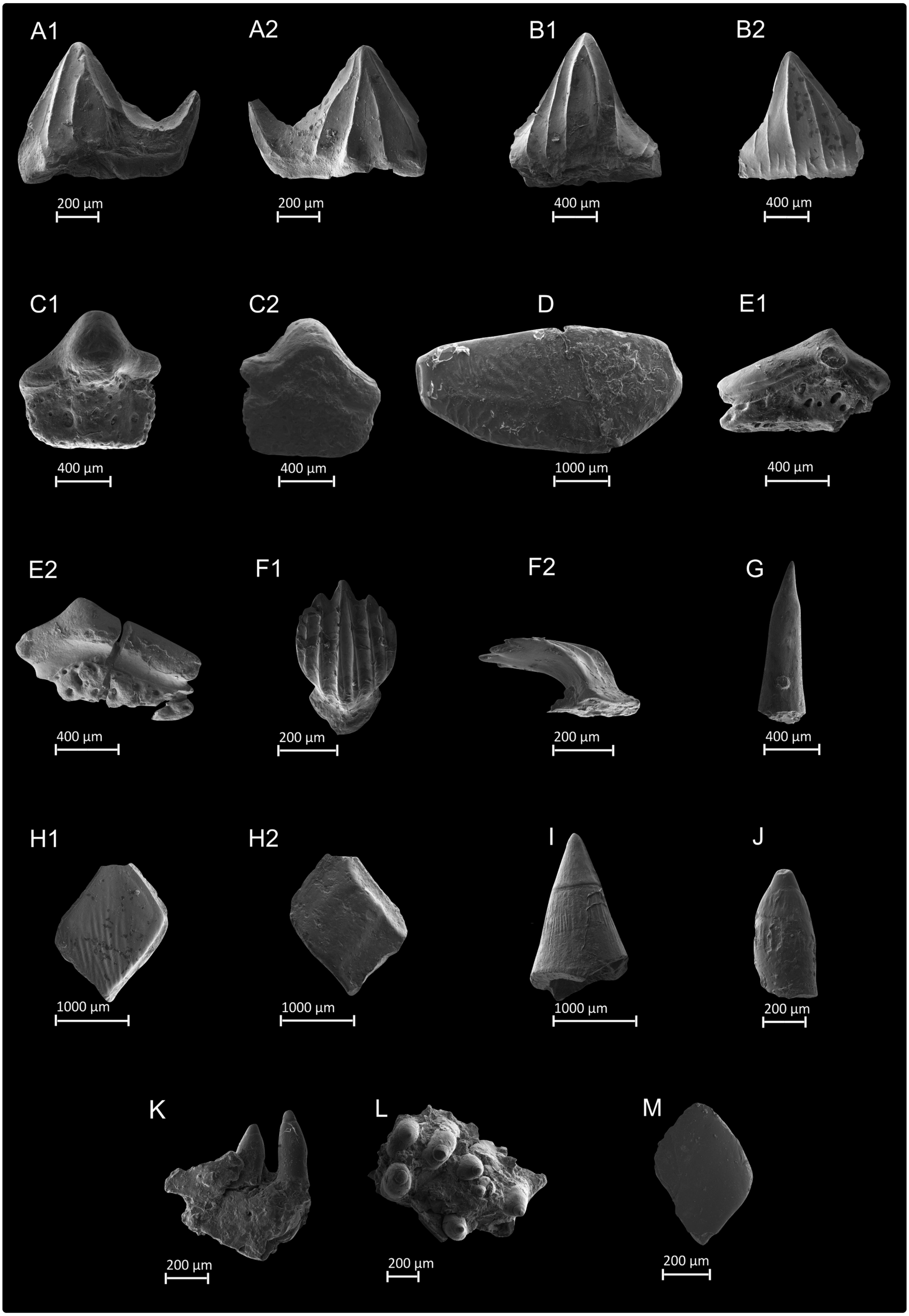

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Fig. 3. Fish microfossils from the glauconite beds at the Miedary locality. A-B, *Polyacrodus keuperianus* teeth. A, ZPAL V.36/09/05. A1, lingual view. A2, labial view. B, ZPAL V.36/09/06. B1, lingual(?) view. B2, labial(?) view. C-D, *Acrodus* cf. *lateralis* teeth. C, ZPAL V.36/09/03. C1, lingual view. C2, labial view. D, ZPAL V.36/09/02 – occlusal view. E, *Lissodus nodosus* tooth. E, ZPAL V.36/09/04. E1, labial view. E2, lingual view. F, indetermined placoidal scale (ZPAL V.36/09/09). F1, lateral view. F2, external surface. G-H, cf. *Gyrolepis*. G, tooth (ZPAL V.36/09/11). H, scale (ZPAL V.36/09/12). H1, external surface. H2, Internal surface. I, *Saurichthys* sp. tooth (ZPAL V.36/09/17.) J-L, *Serrolepis suevicus*. J. teeth (ZPAL V.36/09/18). K, jaw part (ZPAL V.36/09/19), lateral view. L, jaw part (ZPAL V.36/09/20), occlusal view. M, cf. Redfieldiiformes scale (ZPAL V.36/09/14), external surface.

cf. Redfieldiiformes Berg, 1940.

Material: 107 scales (numbered specimen: ZPAL V.36/09/14, Fig. 3M).

Remarks: Ganoid scales with smooth surface and edges. They are the second most common microfossils in the assemblage from glauconite beds and represented by 107 specimens (ZPAL V.36/09/14, Fig. 3M). Like specimens referred to cf. *Gyrolepis, t*his assignment is tentativebecause other groups of actinopterygians have scales with similar morphology (e.g. scales on the posterior part of 'perleidiforms' trunks, compare: Lombardo et al., 2008; Mutter and Herzog, 2004).

Saurichthys sp. Agassiz, 1834.

Material: Seven conical teeth (ZPAL V.36/09/17; Fig. 3I).

Remarks: Teeth have prominent apicobasal ridges on the base, and high acrodin caps with two smooth cutting edges. The border between the cap and the base is sharp. In the most complete specimens, the cap occupies about 30% of the tooth height.

Serrolepis suevicus Dames, 1888.

Material: Six teeth (ZPAL V.36/09/18; Fig. 3J), six jaw fragments with attached teeth (ZPAL V.36/09/19–20; Fig. 3K-L), and six scales (ZPAL V.36/704–705; Fig. 4B-C).

Remarks: The scales are deep, with a prominent dorsal peg and a serrated posterior margin. All specimens are preserved on rock surfaces and the morphology of their internal surface remains unknown. The teeth are peg-like with low and blunted acrodin caps. Subtle ornamentation composed of minute apicobasal ridges is visible on some specimens.

'*Thelodus*' Schmidt, 1861.

Material: Seven teeth.

Remarks: Conical, sigmoidally curved teeth, with blunted acrodin caps, and ornament composed of apicobasal ridges, are traditionally referred to this enigmatic genus. '*Thelodus*' teeth and part of jaws are known from the Muschelkalk deposits of Germany (Böttcher, 2015). However, the name established by Schmidt (1861) is invalid, as it is a homonym of the previously named agnathan genus *Thelodus* Agassiz, 1839.

Ptychoceratodus sp. Jaekel, 1926

Material: Prearticular dental plate attached to the bone (ZPAL V.36/700a; Fig. 4F).

Remarks: It is the only sarcopterygian recognized in the glauconite beds. The dental plate has three completely preserved anteriormost ridges arising from the conspicuous mediolingual junction. Only the lingual-most part of the fourth ridge is preserved due to incompleteness of the posterior part of the plate. The plate is high-crowned and has deep furrows. The ridges are slender and acute. The internal angle of the plate is about 90°.

4.1.2. Dolomite beds

Palaeobates angustissimus Agassiz, 1838.

Material: 119 teeth (ZPAL V.36/2, ZPAL V.36/10/08, ZPAL V.36/10/09; Fig. 5C – D1, 2, Fig. 4D).

Remarks: Crushing teeth with convex surface, covered with more or less conspicuous ornament, comprising minute apicobasal ridges and randomly arranged pits. Dimensions of the teeth occlusal surfaces range from roughly isometric, through pentagonal, to those that are strongly elongated. *P. angustissimus* teeth are the most numerous elasmobranch remains from the dolomite beds.

Hybodus plicatilis Agassiz, 1843.

Material: One tooth (ZPAL V.36/10/02; Fig. 5A1, A2).

Remarks: The tooth has multicuspid crown and a highly porous root. The crown has a centrally located main cusp and lateral cusplets on its sides, respectively three and two. The slopes of the main cusp are very steep. All cusps are ornamented with densely arranged apicobasal ridges. The furrows between the cusps are very deep and almost contact the root.

Acrodus cf. *lateralis* Agassiz, 1839.

Material: Three teeth, ZPAL V.36/10/01; Fig. 5B).

Remarks: These are morphologically indistinguishable from specimens from the glauconite beds. Represented only by the first morphotype of loaf-shaped teeth.

Lissodus nodosus Seilacher, 1943.

Material: 61 teeth (ZPAL V.36/10/03; Fig. 5E1, 2).

Remarks: These teeth are very similar to those described from the glauconite beds. However, they are significantly larger, and most of the specimens bear ornament.

Hybodontiformes indet. Patterson, 1966

Material: One placoid scale (ZPAL V.36/10/15; Fig. 5F 1,2) and three parts of fin spines (ZPAL V.36/10/14; Fig. 5G).

Remarks: The morphology of the fin spines fragment is the same as for the specimen from the glauconite beds. The scale has an inconspicuous neck, whereas its crown forms a roughly round bulge.

cf. *Gyrolepis* Agassiz, 1935.

Material: 123 scales and 70 teeth (ZPAL V.36/10/20, ZPAL V.36/10/21; Fig. 5H – I).

Remarks: The fossils share characters with the cf. *Gyrolepis* specimens from the glauconite beds. The noteworthy feature of the scales is their relatively large size (> 3 mm in diameter).

cf. Redfieldiiformes Berg, 1940.

Material: 215 scales (ZPAL V.36/10/24; Fig. 5N1, 2).

Remarks: As in the case of the cf. *Gyrolepis* remains, these specimens do not differ morphologically from their glauconite beds equivalents. Specimens from the dolomite beds are also relatively large.

Saurichthys sp. Agassiz, 1834.

Material: 34 teeth (ZPAL V.36/10/26; Fig. 5J), and rostral part of the jaw (ZPAL V.36/20; Fig. 4E1,2).

Remarks: The jaw fragment is part of the rostro-premaxillary or dentary. It bears two types of teeth: large and more pointed teeth, distributed in a single row at roughly regular intervals, and small, irregularly distributed teeth, occurring abundantly between the larger ones. Morphologically, the teeth in the jaw resemble isolated teeth found in both dolomite and glauconite beds.

'*Thelodus*' Schmidt, 1861.

Material: Four teeth (ZPAL V.36/10/29; Fig. 5O).

Remarks: The specimens have the same morphology as the '*Thelodus*' teeth from the glauconite beds, apart from their average larger size.

Colobodus sp. Agassiz, 1844.

Material: Three molariform teeth (ZPAL V.36/10/19; Fig. 5K1, 2).

Remarks: Button-like teeth with conspicuous apicobasal striations and acrodin cap in the form of a pronounced central tubercle.

cf. Semionotiformes Arambourg and Bertin, 1958.

Material: 33 teeth (ZPAL V.36/10/30; Fig. 5L).

The teeth are round in the occlusal view and have a smooth surface. In some specimens, inconspicuous apicobasal ridges are visible. The central tubercle is variously pronounced. Several specimens represent dental plates, made of two fused teeth (ZPAL V.36/10/32; Fig. 5M). The jaw fragment is equipped with five separated but closely spaced teeth. All teeth in the jaw have a conspicuous central tubercle. We tentatively

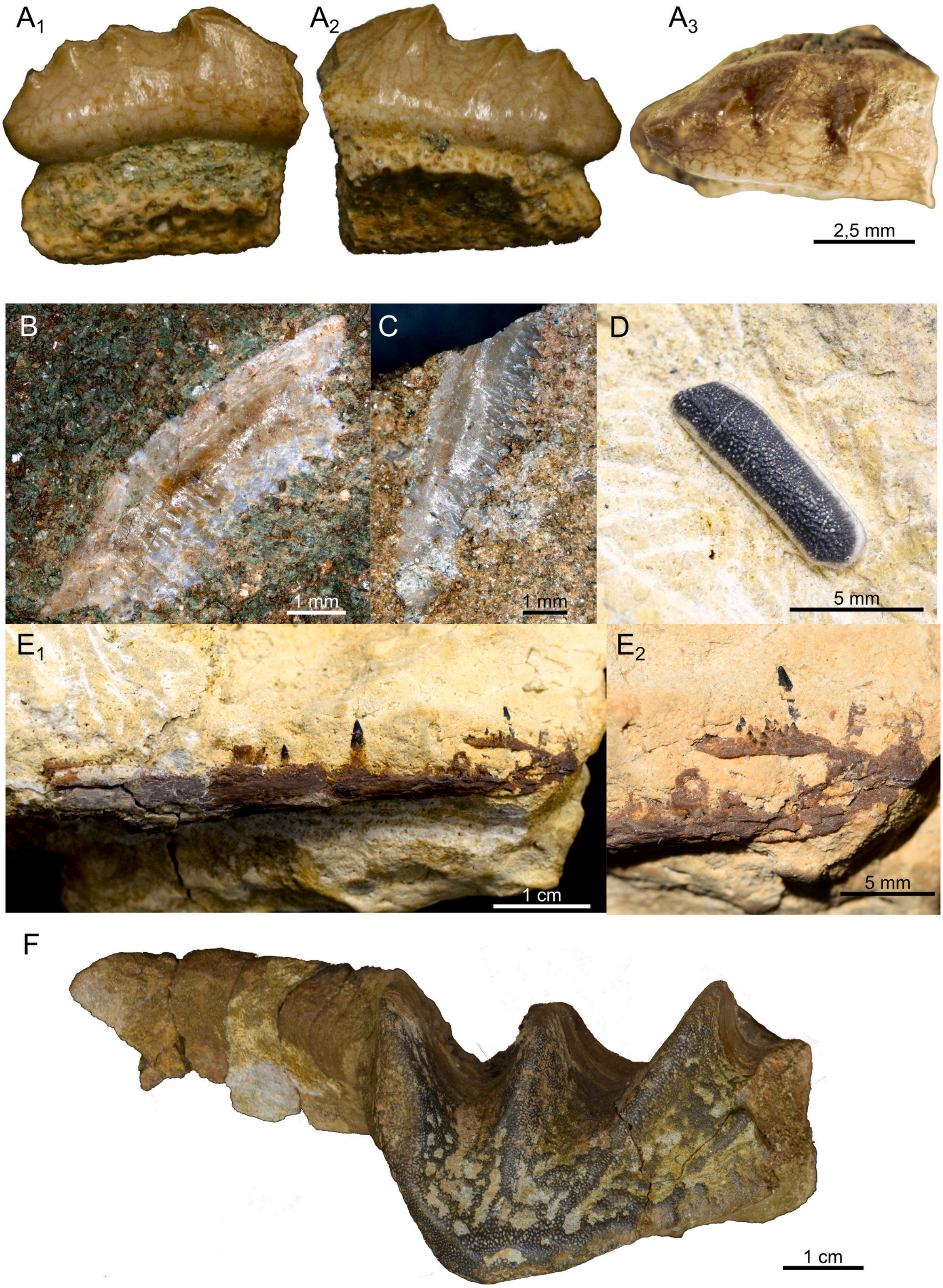

Fig. 4. Fish macrofossils from the Miedary locality. A, *Polyacrodus* cf. *polycyphus* tooth (ZPAL V.36/604. A1, lingual view. A2, labial view. A3, occlusal view. B-C, *Serrolepis suevicus* scales. B, ZPAL V.36/704, external surface. C, ZPAL V.36/705, external surface. D, *Palaeobates angustissimus* tooth (ZPAL V.36/2), occlusal view. E, *Saurichthys* sp. premaxilla or dentary (ZPAL V.36/20). E1, lateral view. E2, dentition. F, *Ptychoceratodus* sp. lower right dental plate (ZPAL V.36/700a), occlusal view.

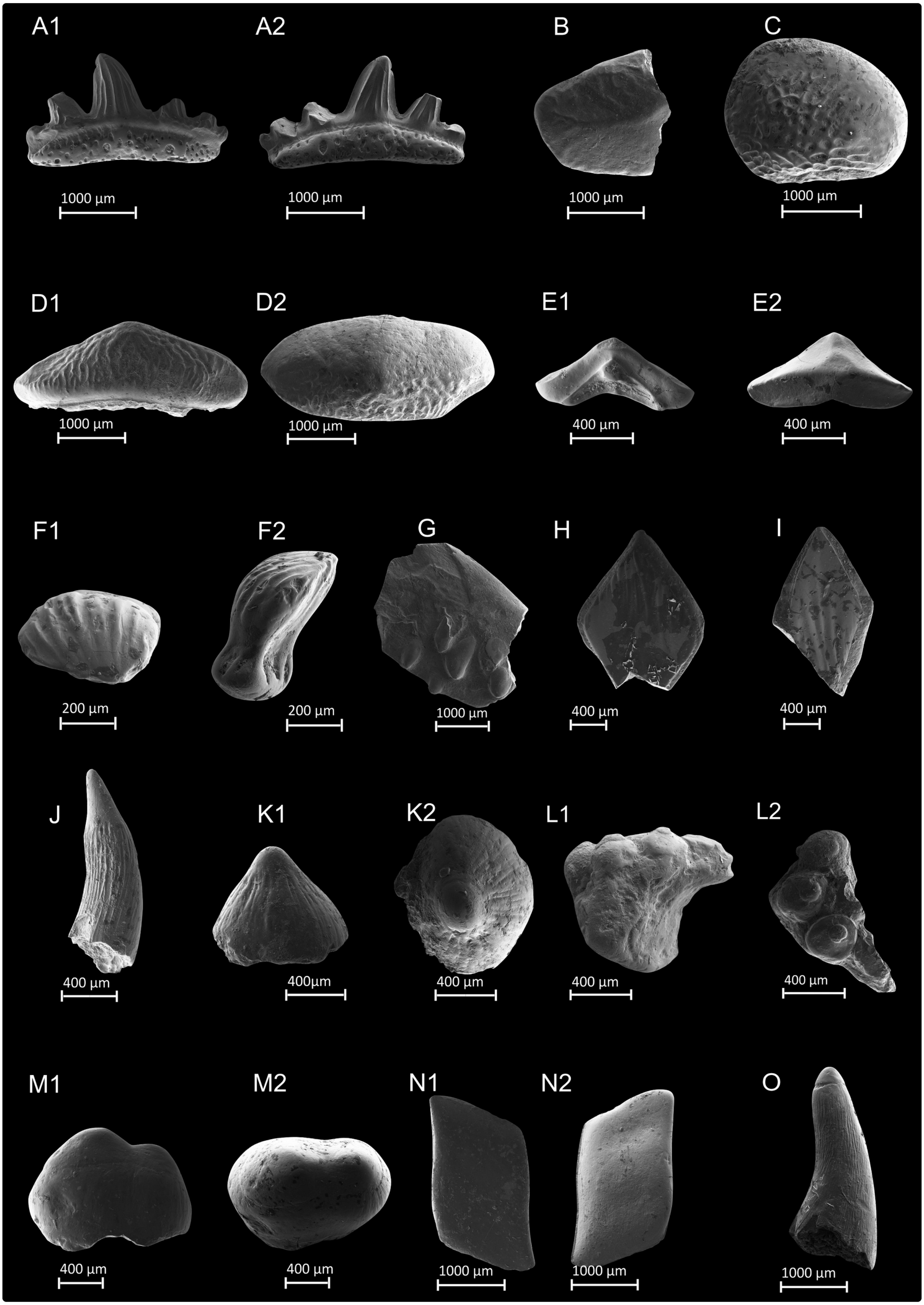

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Fig. 5. Fish microfossils from the dolomitic beds at the Miedary locality. A, *Hybodus plicatilis* tooth (ZPAL V.36/10/02). A1, labial view. A2, lingual view. B, *Acrodus* cf. *lateralis* tooth (ZPAL V.36/10/01), occlusal view. C-D, *Palaeobates angustissimus* teeth. C, ZPAL V.36/10/08, occlusal view. D, ZPAL V.36/10/09. D1, labial view. D2, occlusal view. E, *Lissodus nodosus* tooth (ZPAL V.36/10/04). E1, labial view. E2, lingual view. F, indetermined placoidal scale (ZPAL V.36/10/15). F1, lateral view. F2, external surface. G, indetermined fin spine fragment (*Nemacanthus* sp.?) (ZPAL V.36/10/14). H-I, cf. *Gyrolepis* scales. H. ZPAL V.36/10/20, external surface. I, ZPAL V.36/10/21, external surface. J, *Saurichthys* sp. tooth (ZPAL V.36/10/26). K, *Colobodus* sp. tooth (ZPAL V.36/10/19). K1, lateral view. K2, occlusal view. L-M, cf. Semionotiformes. L, jaw part (ZPAL V.36/10/30). L1, lateral view. L2, occlusal view. M. dental plate (ZPAL V.36/10/32). M1, lateral view. M2, occlusal view. N, cf. Redfieldiiformes scale (ZPAL V.36/10/24). N1, external surface. N2, internal surface. O, "*Thelodus*" tooth (ZPAL V.36/10/29).

assign these remains to Semionotiformes, following the most common identification of such fossils. They may truly represent semionotiforms; however, they could also belong to Bobastraniformes or Perleidiformes (Delsate and Duffin, 1999). Collected material is too scarce for determining their affinity with certainty.

4.1.3. *Associated fauna*

Two morphotypes of tetrapod teeth have been identified among microfossils from the glauconite beds, and one morphotype from the dolomite. The latter are oval in cross-section, often curved, with conspicuous apicobasal ridges along the whole height. They belong to some undetermined eusauropterygians (Fig. 6A), most possibly *Nothosaurus* sp., which have been identified by Sulej et al. (2011) from the same layer. Both teeth morphotypes from the glauconite beds are represented by singule specimens. Morphotype A (ZPAL V.36/09/24; Fig. 6B) is laterally flattened, with conspicuous serration, diagnostic for Archosauromorphs (Renesto et al., 2003). Morphotype B (ZPAL V.36/09/25; Fig. 6C1,2) is oval in cross-section with two sharp edges. Its surface is covered with loosely arranged, subtle ridges, converging toward the sharp edge and declining toward the tip. Similar teeth have been recognized by Dorka (2002), but their affinity remains unknown.

4.2. *Composition of the microvertebrate assemblages*

Microvertebrate assemblages from the bulk samples, ZPAL V.36/09 and ZPAL V.36/10, are considerably different (Fig. 7A). To remove the influence of fragmentation on the comparison, we presented abundances of specimens with preserved unpaired structures (e.g. scales with preserved central part, teeth with preserved central cusp), beside the absolute abundances. The flattening rarefaction curves (Fig. 7B) suggest the differences do not result from the sampling bias. Remains of 'palaeopterygians' and stem neopterygians dominate the assemblage from glauconite beds, whereas hybodontid sharks are rather minor component in contrast, in the dolomite beds the contribution of hybodontids is much higher, mainly due to abundance of *Palaeobates* and *Lissodus* remains. The microfossils can be divided quantitatively into four guilds. (1) Taxa specific only to the dolomite beds: *Palaeobates angustissimus*, Eusauropterygia cf. Semionotiformes, *Colobodus* sp., and *Hybodus plicatilis.* (2) Taxa specific only to the glauconite beds: *Serrolepis suevicus* and *Polyacrodus keuperianus.* (3) Taxa present in both assemblages, but only occasionally in the glauconite beds: *Saurichthys* sp. (4) Taxa equally frequent in both assemblages: *Acrodus lateralis*, *Lissodus* sp., "*Thelodus*". Among the unidentified morphotypes of microfossils, most likely belong to various taxa, cf. Redfieldiiformes scales are more frequent in the dolomite beds, whereas cf. *Gyrolepis* scales in the glauconite.

4.3. *Comparative analysis*

Both the Cluster (CA) and Principal Component Analysis (PCA) show a strong relationship between the behavior of the dataset (vertebrate assemblage composition) and presumed paleosalinity. CA yields two main clusters(Fig. 8A). Cluster A is formed by euhaline and polyhaline faunas, together with the Miedary dolomite beds. Polyhaline and euhaline assemblages are mixed within this cluster, but bootstrap values between particular nodes are relatively low, suggesting lack of considerable faunal differences between these two salinity classes. Cluster B contains all freshwater to mesohaline assemblages, together with the Miedary glauconite beds. The freshwater assemblages form a grouping within this cluster that occupies a sister position to all the oligo to mesohaline assemblages. However, bootstrap value between freshwater and brackish clusters is relatively low, showing high similarity between both groups. PCA results show that the first two Principal Components (PCs) account for 65.3% of variance, and exceed the eigenvalue of 0.8 (40.695% and 1.399; 24.645% and 0.847 respectively). In our view, these two PCs mainly reflect differences explainable in the paleoenvironmental terms. The scatter plot of the PC1 against the PC2 and their loadings are presented in Fig. 8C-D. Topology of the scatter plot is coherent with topology of the scatter plot obtained from the NMDS ordination (stress: 0.0488, 20 tries; Fig. 8B). All the euhaline and polyhaline assemblages are close to each other in both scatter plots, together with the Miedary dolomite beds, except for the Raciborowice

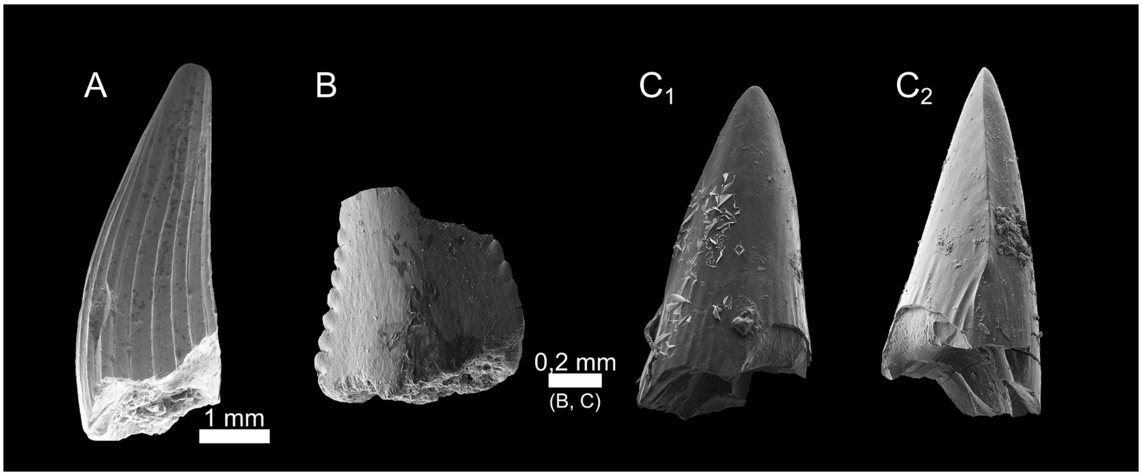

Fig. 6. Tetrapods microfossils from the Miedary locality. A, Eusauropterygia indet. Tooth from the dolomite beds (ZPAL V.36/10/33). B, archosaur tooth from the glauconite beds (ZPAL V.36/09/24). C, indetermined tetrapod tooth from the glauconite beds (ZPAL V.36/09/25). C1, labial or lingual view. C2, mesial or distal view.

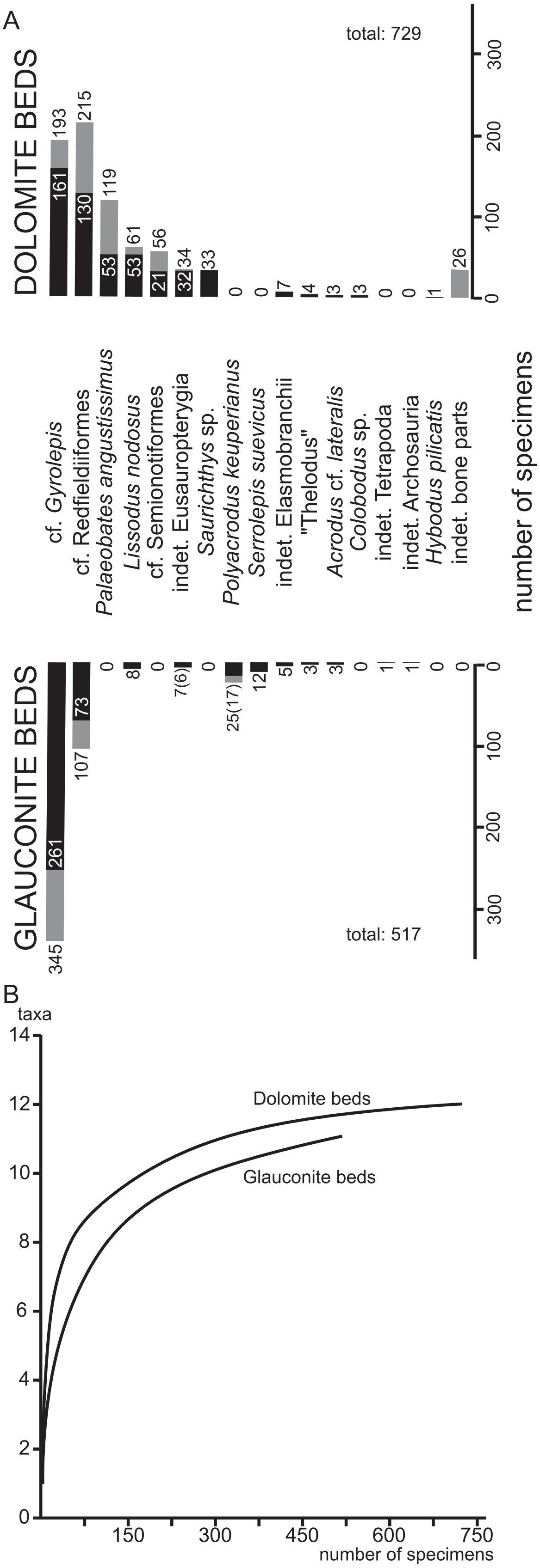

Fig. 7. Quantitative analysis of the microfossil assemblages from the Miedary locality. A. Comparison of the assemblages from the glauconite and dolomite beds. Black bars indicate the mean number of specimens with preserved unpaired structures. B. Rarefaction curves for the both assemblages.

Górne assemblage, which is slightly separated from the others. The oligohaline to mesohaline assemblages and Miedery glauconite beds are grouped together. The assemblages E4 and E5 from Vellberg and Albertibank are close to each other in the scatter plots, whereas E4 assemblage is significantly shifted toward the euhaline and polyhaline assemblages. Another separated group is composed of freshwater assemblages from Krasiejów and Lehbergbanks. Assemblages from Krasiejów and Upper Lehrbergbank occupy the same position, as a result of the datasets having the same composition.

Cross-plotting PC1 against PC2 differentiates analyzed assemblages accordingly to paleosalinity (Fig. 8C), making it possible to recognize taxa associated with specific salinities. PC1 differentiates the marine and not fully-marine assemblages, whereas PC2 differentiates the freshwater and not fully-freshwater ones. Therefore, the highest loadings on PC1 are expected for fossils associated with euhaline and polyhaline conditions, and the lowest for fossils that are widely distributed, but do not occurr in high salinity settings. At the same time, the highest loadings on PC2 are expected for widely distributed fossils that do not occur at low salinities, and the lowest for taxa associated with freshwater conditions. *Palaeobates*, *Hybodus*, and *Colobodus* form a conspicuous group restricted to the euhaline and polyhaline assemblages. PCA results show their strong relationship with highly saline environments as well; they have the highest loadings on PC1 (> 0.35), and loadings close to zero on PC2. Two taxa, *Lonchidion* and phytosaurs, are restricted to freshwater assemblages. Their PC1 loadings are higher than −0.15, but not higher than 0, whereas PC2 loadings are very low (< −0.25). Another group, cf. Semionotiformes, have a PC loading pattern intermediate between specifically freshwater and marine taxa, reflecting their distribution in both marine and freshwater assemblages. They have a relatively high PC1 loading (0.20) and the lowest PC2 loading (−0.41). This category probably contains various taxa with different salinity preferences. *Serrolepis* is the only taxon restricted to oligo and mesohaline assemblages. Its occurrence does not overlap with taxa specific for euhaline to polyhaline, or freshwater assemblages. *Serrolepis* has relatively low PC1 loadings (−0.23) and high PC2 loading (0.34).

The taxa with a wider environmental distribution can be divided into three subgroups: those (1) occurring in all environments from euhaline to freshwater, (2) not occurring in low salinity settings, and (3) not occurring in high salinity settngs. To the last group belong the dipnoans and temnospondyls, generally regarded as being associated with freshwater conditions. They are absent only from polyhaline and euhaline deposits. In the pliohaline E4 Vellberg horizon, only plagiosaurs were identified among temnospondyls remains (Schoch and Seegis, 2016). Temnospondyls and dipnoans exhibit the lowest loadings on PC1 (< −0.35) and close to zero on PC2. *Acrodus, Lissodus*, and eusauropterygians belong to the group not occurring in low salinities. They have the highest loadings (>0.4) on PC2 and approaching zero on PC1. *Acrodus*, however, departs from the two others, due to high loading on PC1 (0.35 compared to −0.06 to 0.00 in the case of *Lissodus* and eusauropterygians), and depressed loading on PC2 (0.22 compared to 0.43 to 0.47). *Acrodus* and eusauropterygians are not confined to oligohaline and freshwater deposits. *Saurichthys*, cf. *Gyrolepis*, and cf. Redfieldiiformes exhibit the widest environmental range, and belong to the fully euryhaline taxa. They have loadings close to zero on both PCs, pointing to a lack of preference for any salinity level. The exception is cf. Redfieldiiformes, which has a relatively low PC1 loading (−0.13). However, this could result from an inappropriate sampling of the marine assemblages from Raciborowice Górne and Wolica (see the study limitations section).

5. Discussion

5.1. Fossils distribution and salinity preferences

A crucial question is the relation between the occurrence of taxa in the assemblages, and their true salinity preferences. The straight causal

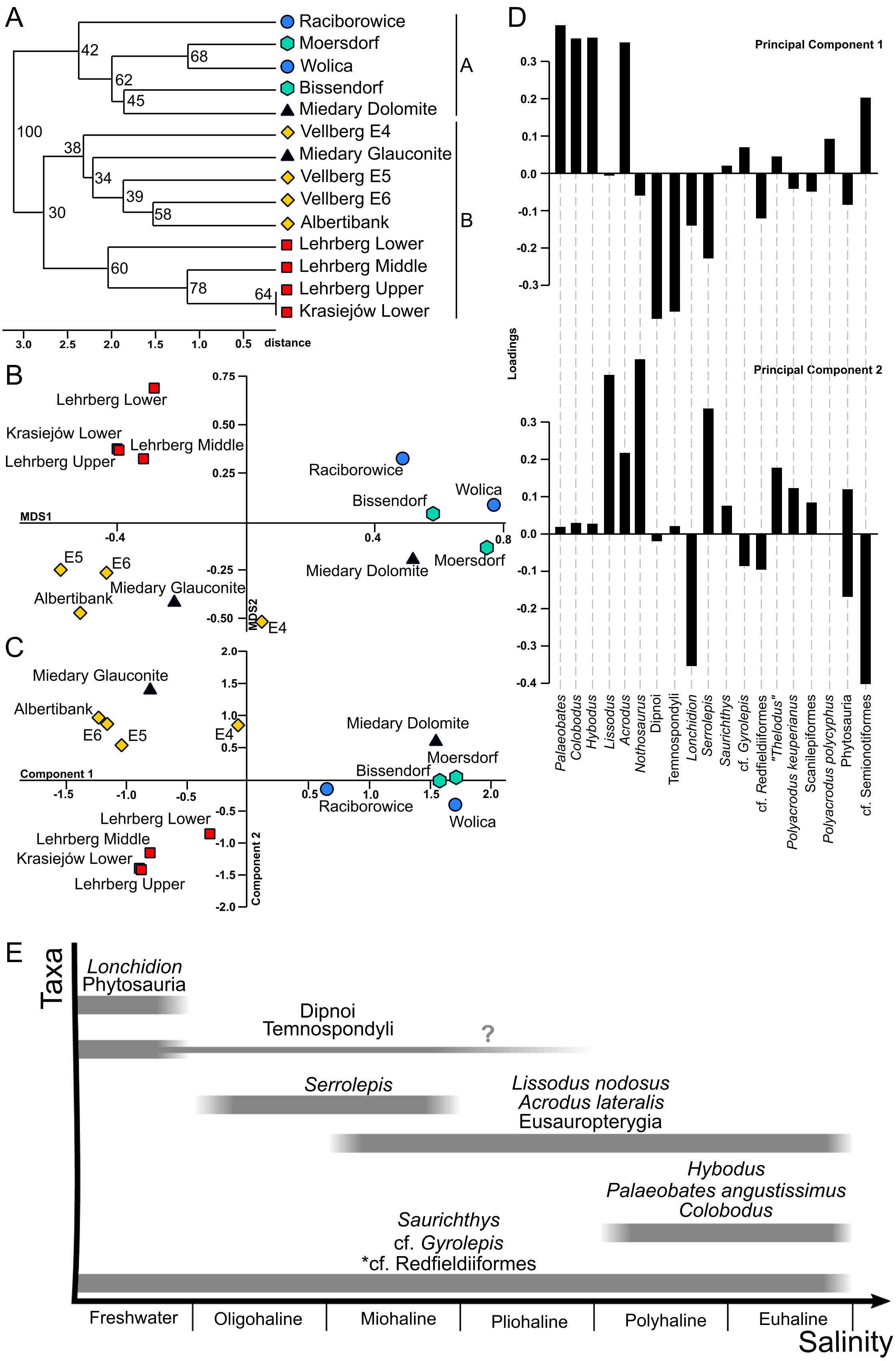

Fig. 8. Comparative analysis of the faunal assemblages from the Middle-Late Triassic of the Germanic Basin. A. Cluster analysis dendrogram. Numbers next to branches indicate bootstrap support. B. Nonmetric Multidimensional Scaling scatter plot. C. Principal Component Analysis scatterplot. D. Loadings for the Principal Components 1 and 2. E. Presumed salinity tolerance of the analyzed taxa from the Germanic Basin during the Middle-Late Triassic.

link between them can be disrupted by the preburial transport of carcasses or the stratigraphic averaging of the assemblages, for example, through the reworking of beds formed under various conditions. We believe that taxa specific for the euhaline to polyhaline assemblages (*Hybodus*, *Palaeobates*, *Colobodus*), those specific for the oligo to miohaline assemblages (*Serrolepis*), those specific for freshwater assemblages (*Lonchidion*, Phytosauria), and those not occurring in low salinity settings (*Acrodus*, *Lissodus*, eusauropterygians) were truly preferring such salinities. Their preburial transport or derivation from other environments is considered unlikely, especially given the repetitive pattern of their occurrences in specific conditions and their absence in others. The more complex cases are taxa not occurring in high salinities settings (Temnospondyli, Dipnoi), because transport of their carcasses from freshwater to brackish environments cannot be safely excluded. *Polyacrodus keuperianus*, *Polyacrodus* cf. *polycyphus*, "*Thelodus*", and Scanilepiformes are hard to interpret in paleoecological terms on the basis of our analyses, since they are confined to one assemblage and absent in others with similar paleosalinities. *P. keuperianus* is known from Lower Keuper localities not included in the analysis and from the Schilfsandstein (Dorka, 2002), suggesting relationships with more freshwater environments.

The taxa considered here as not associated with low salinities (*Acrodus*, *Lissodus*, eusauropterygians) are usually believed to be specific for fully marine environments (Diedrich, 2009; Botfalvai et al., 2019). The case of *Lissodus* is especially surprising because according to previous studies on the stratigraphic distribution of these sharks within the Germanic Basin (Liszkowski, 1993), it is abundant within the Lower Muschelkalk and rather rare in the Upper Muschelkalk, whereas our data show an exactly opposite pattern, suggesting a preference for non-fully marine salinities. Nevertheless, this genus clearly does not occur in fully freshwater deposits. Also, eusauropterygian are usually regarded as being mainly marine reptiles. Their lack in the assemblages from Raciborowice Górne and Wolica is rather artificial and caused by insufficient sampling (see the study limitations section). Perhaps eusauropterygian preferences were similar to those of extant marine reptiles (like Hydrophiinae sea snakes or *Crocodylus porosus*), which exhibit a wide salinity tolerance and ability to migrate through brackish or freshwater environments, despite spending a significant part or most of their lifespan in more saline conditions (Rasmussen, 2001; Letnic and Connors, 2006). Distribution of eusauropterygians fossils in Miedary suggests a change in environmental preferences during their lifespan. Mature specimens of *Nothosaurus* sp. are present in both assemblages, whereas eusauropterygians micro teeth are present only in the dolomite beds. Lack of *Nothosaurus* sp. microfossils in the glauconite beds may reflect the avoidance of less saline environments by young individuals or their low mortality there.

Taxa occurring in all salinity levels (cf. *Gyrolepis*, cf. Redfieldiiformes) are mostly collective categories, and their apparent wide preferences may result from difficulties in the reliable identification of the isolated remains. Most probably the same reasons are responsible for peculiar behavior of cf. Semionotiformes in the PC analysis. *Saurichthys* may be the only truly euhaline genus included in the analysis, which would be consistent with previous studies of these fish (Romano et al., 2012).

The ratio of stenohaline to euryhaline taxa shows the dominance of the former, especially after collective categories are excluded. This suggests a significant taxonomic separation of environments with different salinities, at least at the specific level. Our results contrast with studies on aquatic vertebrate faunas from Pennsylvanian assemblages, which exhibit an opposite pattern, i.e., a dominance of euryhaline species and a similar taxonomic composition in freshwater and marine deposits (Carpenter et al., 2015; Ó Gogáin et al., 2016). This homogeneity probably reflects dominance by species occasionally migrating into freshwater from the marine realms, and therefore representing the stage preceding the formation of ecosystems composed of vertebrates being the permanent inhabitants of freshwater reservoirs (Carpenter et al., 2015; Ó Gogáin et al., 2016). The Middle-Late Triassic vertebrates seems to exhibit a clear separation of groups preferring freshwater and marine conditions. A novelty is presence of potential brackish specialists, revealing another step in the ecological specialization of fish along the salinity spectrum. According to Hagdorn and Mutter (2011), this niche would be occupied by *Dipteronotus* even in the Early Triassic.

5.2. Origin and environment of the faunas from Miedary

A change in the salinity-related composition of fish communites is evident in the Miedary fossil assemblages. The assemblage from dolomite beds does not differ from the euhaline to polyhaline assemblages from Muschelkalk, whereas the assemblage from glauconite beds is similar to brackish assemblages from Albertibank and E5-E6 horizons from Vellberg. Considering the generally decreasing salinity within the Germanic Basin during the Ladinian (Franz et al., 2015), we suggest that rather polyhaline conditions existed during the deposition of the dolomite beds. Co-occurrence of the marine-related and freshwater taxa within the glauconite beds suggest that temnospondyls, lungfish, and some other fish remains may represent allogeneic components transported from more freshwater environments. The presumed high-energy origin of the beds supports this hypothesis. Possible reworking of the fossils originally deposited in other lithologies impedes resolving of this issue using a sedimentological approach. Hypothetical reworked freshwater deposits are also a potential source of the freshwater fossils. Allogenic origin of the freshwater species may be tested using geochemical methods or through the taphonomic analysis of macrofossils. Despite the doubtful parautochtonous character of the assemblage, we believe that its composition reflects an important environmental signature. The lack of taxa specific for euhaline or polyhaline conditions, and presence of taxa not associated with freshwater, point to a oligo to mesohaline environment. Furthermore, oligo to miohaline conditions are supported by the occurrence of *Serrolepis suevicus*. However, until data collected using independent methods are available, the brackish character of the Miedary glauconite beds remains unclear.

5.3. *Serrolepis* lakes

Serrolepis suevicus is the only representative of its genus, and most probably belongs to the polzbergids (Hagdorn and Mutter, 2011). Until recently, it was known in the literature only from isolated scales and jaw parts. Hagdorn and Mutter (2011) were the first to pay attention to the environmental significance of this species. They not only noticed that *Serrolepis* is limited to deposits with ambiguous salinity, but also that the Lower Keuper assemblages containing *Serrolepis* are distinct from others. *Serrolepis* is known mainly from four horizons cropping out in the western part of the Germanic Basin (Hagdorn and Mutter, 2011). The assemblages from the Albertibank and the Untere Graue Mergel strata (including E5 and E6 horizons from Vellberg) are composed of polzbergids, saurichthyids, lungfish, capitosaurs, plagiosaurs, nothosaurs, and terrestrial tetrapods. At the same time, they lack typically euhaline taxa like *Palaeobates*, *Colobodus* or *Hybodus*. Occurrences of nothosaurs in these assemblages are relatively rare, as are those of terrestrial tetrapods. The composition of the Sandige Pflanzenschiefer assemblage is slightly different because of the complete lack of nothosaurs, and higher contribution of terrestrial taxa. The vertebrate fauna from Estherienschichten is poorly understood.

Hagdorn and Mutter (2011) proposed the concept of "*Serrolepis* lakes" for environments with these specific faunal assemblages, composed of mixed taxa usually regarded as either freshwater or marine. Our results confirm the specific composition of assemblages containing *Serrolepis*, and show that previously known occurrences of this genus were limited to the oligohaline to miohaline environments. This makes *Serrolepis* a potentially useful indicator of such brackish conditions.

The assemblage from Miedary glauconite beds provides a new record of the *Serrolepis* lake. Its composition is strikingly similar to that of the Albertibank, and E5 and E6 horizons from Vellberg, as supported by our PCA results. However, as mentioned previously, the composition of the vertebrate fauna is the only evidence for brackish conditions, and further studies are required. An interesting part of the analysis is the E4 horizon from Vellberg, which cannot be regarded as a typical *Serrolepis* lake deposit due to the presence of *Nothosaurus* as the most abundant tetrapod, and the simultaneous general absence of temnospondyls (only *Plagiosternum* is present), terrestrial components, *Serrolepis*, *Palaeobates*, *Hybodus*, and *Colobodus*. The E4 horizon seems to represent some intermediate environment between oligo- or miohaline and polyhaline conditions, as suggested already by Schoch and Seegis (2016). It is noteworthy that the particular *Serrolepis*-bearing horizons represent various sedimentological settings, like Miedary glauconite beds and Albertibank.

Are there any possible modern equivalents of the *Serrolepis* lakes? The Baltic Sea and the Black Sea are classic examples of present-day brackish basins. The salinity of the Black Sea (17–18‰) is much higher than the Baltic (6–7‰) (Leppäkoski and Mihnea, 1996). As a result, the freshwater species are permanent inhabitants of the miohaline (Remane and Schlieper, 1972) Baltic Sea, whereas they inhabit only rivers' mouths areas in the pliohaline/polyhaline Black Sea. Numerous marine fish species can colonize polyhaline and mesohaline reservoirs, but with further salinity reduction, their ability to spawn, reproductive success, and survivorship decrease (Ojaveer and Kalejs, 2005). A significantly lower number of species tolerant of euhaline conditions live in miohaline or oligohaline waters (Remane and Schlieper, 1972). In this context, the Triassic *Serrolepis* lakes were more similar to miohaline or oligohaline than to pliohaline or polyhaline reservoirs, due to the presence of probably freshwater temnospondyls and dipnoans, and only some euhaline taxa tolerant that could tolerate depressed salinity.

5.4. Limitations of the comparative study and perspectives

Our analysis has several limitations resulting from, for example, the lack of data about fossils frequencies in particular assemblages. These may vary significantly, as in the case of *Saurichthys* or *Lissodus* from Miedary (Fig. 7). Its consequence is not only loss of a potentially important environmental signal, but also the inclusion some incidental occurrences into the analyses. Poor preservation or lack of diagnostic features can result in taxonomic inaccuracy. The applies especially to cf. *Gyrolepis*, cf. Redfieldiiformes, and cf. Semionotiformes, which almost certainly encompass cryptic diversity, unrecognizable until more complete specimens are found. Another limitation is that the assemblage composition provides information about local depositional conditions, but not necessarily about the actual life environment of the species. An example is provided by temnospondyl amphibians and dipnoans (see section 'fossil distribution and salinity preferences'). Testing this limitation requires application of more sophisticated geochemical methods, such as stable isotope analyses or mineralogical studies on bones infills.

The last factor that may bias our results is the insufficient sampling of the bonebeds resulting in the underestimation of faunal diversity. This strongly depends on the method used to obtain the fossils. Microfossils from Bissendorf, Miedary, Moersdorf, and Wolica were collected through the similar method from disaggregated wet-sieved samples of large sediment portions (Liszkowski, 1973; Delsate and Duffin, 1999; Diedrich, 2009). Fossils from Lehrbergbanks, Albertibank, and Vellberg were collected during the long-term surface collecting and occasional excavations. Both methods we regard as reliable for getting roughly representative insights to assemblage composition. Unfortunately, the description of the assemblage from Wolica focused on the fish teeth (Liszkowski, 1973). Therefore, we suspect that components not represented by such remains may have been omitted. Difficulties occur in case of the assemblage from Raciborowice Górne. The method of fossils collecting from this site is not explained, although the count of the described specimens suggest a small sample (Chrząstek, 2008). Summarizing, we guess that our understanding of the diversity of assemblages from Raciborowice Górne and Wolica may be significantly incomplete and lack important components.

5.5. Conclusions

The results of this study show the dependence between vertebrate assemblage composition and salinity, inferred from the independent sources. Particular taxa exhibit various patterns that can be related to saline conditions. We recognized three groups of stenohaline vertebrates: (1) specific to marine (euhaline and polyhaline) conditions, namely *Palaeobates angustissimus*, *Hybodus plicatilis*, and *Colobodus*; (2) specific for oligo to miohaline conditions, namely *Serrolepis suevicus*, and (3) specific for freshwater conditions, namely Phytosauria and *Lonchidion*. These stenohaline taxa can be regarded as potential paleosalinity indicators. However, the remains of freshwater organisms are easily transported into the more saline environments, and their fossils should therefore not be regarded as absolute environmental indicators. Eusauropterygians, *Acrodus* cf. *lateralis*, and *Lissodus* are believed to be euryhaline taxa, occurring in various paleosalinities, in additon to fully freshwater and oligohaline. *Saurichthys* has the widest preferences among analyzed taxa, and is not related with any particular kind of saline regime. The present study confirms the oligo to mesohaline signature of *Serrolepis* lake communities, comprising the polzbergid *Serrolepis suvicus*, and a mixed assemblage of vertebrates usually believed to be specific for marine and freshwater environments. In general, the contribution of euryhaline taxa in the Middle-Late Triassic vertebrate faunas is relatively low. The assemblages examined in this study demonstrate a clear separation of species specialized to freshwater and marine conditions.

Research into two vertebrate-bearing horizons in Miedary, mainly in terms of microfossil content, show the existence of diverse fish assemblages within both layers. The assemblage from glauconite beds consists 4 hybodonts (*Acrodus* cf. *lateralis*, *Lissodus nodosus*, *Polyacrodus keuperianus*, *Polyacrodus* cf. *polycyphus*), 5 actinopterygians (cf. *Gyrolepis*, cf. Redfieldiiformes, *Saurichthys* sp., *Serrolepis suevicus*, "*Thelodus*") and sarcopterygian (*Ptychoceratodus* sp.), accompanied by previously described eusauropterygians, and temnospondyls. The assemblage from dolomite beds consists 4 hybodonts (*Acrodus* cf. *lateralis, Hybodus plicatilis*, *Lissodus nodosus*, *Palaeobates angustissimus*), 6 actinopterygians (*Colobodus* sp., *Gyrolepis*, cf. Redfieldiiformes, *Saurichthys* sp., cf. Semionotiformes, "*Thelodus*"), and eusauropterygians represented by microfossil teeth. The comparison with other vertebrate assemblages suggests polyhaline conditions during formation of the dolomite beds, and oligo to miohaline during formation of the glauconite beds. The assemblage from glauconite beds represents a new occurrence of the *Serrolepis* lake community, the first in the eastern part of the Germanic Basin.Acknowledgments.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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