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ARTICLE

# AN UPPER TRIASSIC TERRESTRIAL VERTEBRATE ASSEMBLAGE FROM THE FORGOTTEN KOCURY LOCALITY (POLAND) WITH A NEW AETOSAUR TAXON

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ABSTRACT—Since 1990, several localities within the Keuper (upper Middle to Upper Triassic) strata in southern Poland have yielded remains of numerous terrestrial vertebrate species. Here we report a new Upper Triassic vertebrate assemblage from the rediscovered Kocury locality. An incomplete theropod dinosaur fibula named *Velocipes guerichi* described in 1932 was found there. The site was then forgotten and not explored until our excavations began in 2012, that yielded material of a lungfish, a proterochersid turtle, and a new typothoracin aetosaur *Kocurypelta silvestris* gen. et sp. nov. The new taxon is characterized by autapomorphies of the maxilla: an elongated edentulous posterior portion longer than 80% of the posterior maxillary process, a short medial shelf restricted to the posterior portion of the bone, an anteriorly unroofed maxillary accessory cavity, and lack of a distinct groove for choanal recess on the anteromedial surface of the bone. These new finds improve our knowledge on the vertebrate diversity of the Germanic Basin in the Late Triassic, evidencing the presence of yet unrecognized taxa. Additionally, the partial cranial aetosaur material emphasizes the issues with the aetosaurian taxonomy that is focused mostly on the osteoderm morphology.

http://zoobank.org/urn:lsid:zoobank.org:pub:C8AAB89F-A36F-407D-8E2E-491C324F02F3

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#### INTRODUCTION

Two decades of intensive fieldwork resulted in numerous discoveries of the Upper Triassic vertebrate assemblages in the Keuper strata of southern Poland that belong to the eastern part of the Germanic Basin. Five localities have been discovered so far, namely Krasiejów, Lisowice, Woźniki, Poreba, and Zawiercie-Marciszów. They cover an area extending from west to east for a distance of about 90 kilometers (Fig. 1). Despite their geographic proximity, they display surprising taxonomic diversity and clear differences, especially regarding vertebrates (Dzik et al., 2001, 2008; Budziszewska-Karwowska et al., 2010; Sulej et al., 2011a, 2012).

The discussion about the paleoenvironments and stratigraphy of these localities has already received considerable attention (e.g., Zatoń and Piechota, 2003; Szulc, 2005; Zatoń et al., 2005, 2015; Szulc et al., 2006, 2017; Dzik and Sulej, 2007, 2016; Dzik et al., 2008; Gruszka and Zieliński, 2008; Marynowski and Simoneit, 2009; Skawina, 2010, 2013; Sulej et al., 2011a, 2011b, 2012, 2020; Bodzioch and Kowal-Linka, 2012; Konietzko-Meier and Klein, 2013; Konietzko-Meier and Sander, 2013; Pacyna, 2014,

2019; Środoń et al., 2014; Świło et al., 2014; Fijałkowska-Mader et al., 2015; Kubik et al., 2015; Philippe et al., 2015; Jewuła et al., 2019; Kowalski et al., 2019). Two main hypotheses explaining the assemblage differences have been proposed. The first is based mainly on lithostratigraphic and chemostratigraphic correlations with climatic data. These data suggest that all five localities represent a relatively narrow time frame encompassing the early-mid Norian (Szulc and Racki, 2015; Szulc et al., 2015a, 2015b). Therefore, the observed faunal variability would be mainly controlled by environmental factors. The second hypothesis is based on biostratigraphic correlations (on vertebrates and spinicaudatans), and suggests large temporal differences (Carnian to the latest Norian/early Rhaetian) among some of the localities (Dzik et al., 2000; Dzik, 2001; Olempska, 2004; Kozur and Weems, 2010; Geyer and Kelber, 2018). Unfortunately, radiostratigraphic data are available only from Lisowice and indicate the age no older than the late Norian (Kowal-Linka et al., 2019). Paleomagnetic data from the Krasiejów horizon most probably correlates it with the latest Tuvalian (Carnian) polarity record (Nawrocki et al., 2015).

If the assemblage differences observed between these localities are a good reflection of faunal diversity between them, then various environmental (biotic/abiotic) and temporal (evolution, paleobiogeographic changes) factors have to be carefully taken into account to explain their heterogeneity. More specimens and fossiliferous localities are necessary to reduce the effect of sampling

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FIGURE 1. **A**, map of Poland with the main fossil-bearing Keuper localities in Silesia. **B**, geological section of the excavations in the Kocury site. **C**, **D**, thin section of the conglomerate from Kocury, with visible quartz grains (Q), sparite- (S) and micrite-like (M) cement and oncoid (O).

bias, before considering other causes for the observed disparities. Therefore, we describe here a new Upper Triassic vertebrate assemblage from the rediscovered locality of Kocury near Dobrodzień (Silesia, Poland) that increases our knowledge about taxonomic diversity in the Germanic Basin.

The Kocury ('Koczurren', 'Koczury', 'Koczurry', or 'Kotzuren' in the historical transcription) site was explored geologically for the first time in the 19th century and since then only briefly mentioned in the literature (von Carnall, 1843, 1846; Göppert and Roemer, 1858; Roemer, 1862, 1863). Roemer (1870) presented the first description of a fossil originating from the Kocury site -an isolated tooth referred to the phytosaur Termatosaurus albertii Meyer and Plieninger, 1844. The current whereabouts of this specimen are unknown. In the second half of the 19th century, the site was studied by the German paleontologist Georg Gürich, born in 1859 in the nearby town of Dobrodzień (Gürich, 1884, 1890; Wysogórski, 1933; Dzik, 2003b). During the exploration of the adjacent Upper Silesia Triassic strata he collected vertebrate fossils from the quarry in the Kocury forest. A partial limb bone, later transported by Gürich to the University of Hamburg, was described by Friedrich von Huene as a new taxon of a theropod dinosaur, Velocipes guerichi von Huene, 1932. The specimen, thought to be destroyed during World War II, was rediscovered recently in the collection of the University of Hamburg, and reexamined (Skawiński et al., 2017). The details on the origin site yielding V. guerichi material were preserved on the collection label associated with the specimen, enabling us to rediscover the Triassic strata in Kocury in 2012.

Here, we describe the vertebrate material collected from this locality so far, and compare its environmental data and taxonomic composition of the vertebrates with those from other Triassic localities in Poland.

Institutional Abbreviations-CSMM, Carl-Schweizer-Museum Murrhardt, Murrhardt, Germany; GPIM UH, Geological-Palaeontological Institute and Museum of the University of Hamburg, Hamburg, Germany; NHMUK, Natural History Museum, London, U.K.; PEFO, Petrified Forest National Park, Petrified Forest, Arizona, U.S.A.; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; TMM, Texas Vertebrate Paleontology Collections, University of Texas, Austin, Texas, U.S.A.; TTUP, Texas Tech University Museum, Lubbock, Texas, U.S.A.; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.; UFSM, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

#### GEOLOGICAL SETTING

The geology of the Kocury site was mentioned for the first time by the Prussian geologist Rudolf von Carnall, who described the uncovered strata as "the most westward lying outcrop of the Jurassic limestones [in the Upper Silesia Region]" (von Carnall, 1843:424) that was marked on his geological map (von Carnall, 1844). Later, the lithology of the strata was described in more detail, with an emphasis on the discovery of limestone breccia, based on the section in a small quarry and data recovered by drillings (von Carnall, 1846). In the following years, the breccia from Kocury was mentioned in the literature several times (Göppert and Roemer, 1858; Roemer, 1862, 1863) until it was assigned to the 'Lisów Breccia' (Lissauer Breccia) by Roemer (1870). Von Huene assigned the 'Lisów Breccia' to the Middle Keuper without further explanation (von Huene, 1932).

The recent excavation site is located east of Kocury village (Skawiński et al., 2017). It lies in south-western Poland, in the Silesia region, 40 km north-east of Opole and 6 km north of Dobrodzień (Fig. 1A). The Keuper strata crop out around Kocury, usually covered only by a thin layer of soil. In the past, there were two small quarries located within a 700 meter radius of the rediscovered site, which have been abandoned since, flooded, and covered with a dense forest. Therefore, no exposure exists there, and an excavator was necessary to remove the vegetation and soil above the fossiliferous strata.

The geological section (Fig. 1B) is dominated by reddish, greenish, and grayish claystones and mudstones that do not display any prominent lamination and are up to 3 m thick. They are interrupted by gravish polymictic conglomerates up to 1.5 m thick, with concave erosive bases. Most of the observed clasts are rather small (up to 15 mm) and rounded. The diameter of the clasts varies within the succession. The horizons with smaller clasts interweave with the rest of the bed that is characterized by relatively thicker pebbles. This difference in size among clasts might be an indicator of changing energy of environment during the deposition (McLaren, 1981). The conglomerates are generally poorly sorted. The pebbles have various lithology: fragments of sandstones, limestones, claystones, and rare quartz grains. Additionally, fossil bones, oncoids, and shells of bivalves have been found in the conglomerates. The cement that holds the clasts is calcitic. So far, we have identified sparite- and micrite-like cements. These conglomerates are sometimes bounded by a layer of loose conglomerate with a clayish matrix and very rare fossil wood fragments.

The portion of the conglomerate preserved at the proximal tip of the *Velocipes guerichi* specimen GPIM UH no. 252 collected there in the 19th century (von Huene, 1932; Skawiński et al., 2017) is similar to that exposed in Kocury during our excavations. Hence, it is plausible that the specimen was collected from the strata similar to these described herein, likely from one of the nearby quarries.

All the collected fossil bones are preserved in a similar way and apparently come from a similar sedimentary environment, suggesting a common age and origin. They are all black or dark brown, disarticulated, and often broken. However, their surface is usually not eroded: fine structures are well preserved in some specimens. This suggests a relatively short transport and no redeposition (Behrensmeyer, 1982; Holz and Barberna, 1994). The oncoids are small and poorly developed if compared with similar structures from the Lisowice and Poreba localities (see Szulc et al., 2006, 2015a, 2015b; Sulej et al., 2012; Tałanda et al., 2017; Bornemann, 1887, also described oncoids from the 'Lisów Breccia' of Koszęcin). They are also much less common at Kocury. Based on their orientation in the conglomerate, and damage observed on their surfaces, it seems that they were buried away from the place of their formation. The oncoids are often composed of just a few laminae (Fig. 1D), which means that the conditions enabling their formation lasted for a relatively short time.

In general, the depositional environment of the Kocury vertebrate assemblage resembles that of Poreba. Both fossil associations were discovered inside poorly sorted conglomerates (Sulej et al., 2012; Szczygielski and Sulej, 2016). The coarse-grained sediments are also present in Woźniki, Lisowice, and Krasiejów

(Szulc, 2005; Szulc et al., 2006; Sulej et al., 2011a; Tałanda et al., 2017). However, most of bones found in these three localities come from the fine-grained beds, thus from completely different depositional regimes than the high energy environments represented in Poreba and Kocury. The bone-bearing conglomerates in Poreba consist mainly of carbonate nodules, bivalve shells, oncoids, and wood fragments. Quartzite pebbles and lithoclasts of igneous rocks are rare. Such composition suggests intraformational deposits (Szulc, 2005). Detailed study on the mineralogical composition of the conglomerates from Kocury is beyond the scope of this paper. However, our preliminary observations suggest significant differences in grains composition between Kocury and Poreba that suggest different supply areas for these conglomerates. In the conglomerates from Kocury we found numerous quartzite grains, while wood fragments, oncoids, and bivalve shells are very rare.

On the basis of micro- and macroscopic observations, we preliminarily propose a two-stage scenario of the Kocury conglomerates formation. The first stage is infilling of channels formed by the fluvial system with gravel. The second is lithification of the gravel by calcite cement, due to migration of ground-solutions through the deposits. The diversified cement structure (micrite- and sparite-like) suggests a more complex scenario of the lithification. The formation of the carbonate matrix in fluvial sediments is related with post-depositional circumstances, and the timing of this process varies. However, the proposed caliche-like formation of the carbonate matrix is typical in dry and semi-dry climates, therefore congruent with possible influence of an aeolian environment. It is compliant with the research carried out at the other Upper Triassic localities (Gardner, 1972; Schlesinger, 1985; Jewuła et al., 2019). However, more sophisticated geochemistry methods had not been applied yet, hence the strict model of the conglomerate formation is preliminary.

Racki and Szulc (2015) established formal division of the middle Keuper in Silesia, comprising the Grabowa Formation subdivided into three well defined members. Conglomerates are widely distributed within the Silesian Keuper succession, according to observations from drill cores and outcrops; they occur within all subdivisions of the Grabowa Formation (Szulc et al., 2015). Conglomerates also occur above the erosional boundary of the Grabowa Formation, within the informal Połomia Formation (Szulc et al., 2015). Proximity between the Kocury site and the Triassic-Jurassic outcrops boundary, strongly suggests that the discussed section belongs to the upper part of the Keuper succession. Composition of the Kocury conglomerates is clearly different from the Połomia gravels, composed mainly of quartz and quartzite grains (Jakubowski, 1977). Therefore, based on our observations, we regard that the Kocury site possibly belongs to the Patoka Member of the Grabowa Formation.

#### MATERIAL AND METHODS

The fossil material (Table 1) was collected in the excavations during the seasons of 2012–2019. Large blocks of calcareous fossiliferous conglomerates were removed by an excavator and then broken into smaller fragments. All collected specimens are deposited in the Institute of Palaeobiology, Polish Academy of Sciences (Warsaw, Poland).

Three-dimensional models of the specimens (Supplementary Material) were prepared using the Shining 3D EinScan Pro 2X 3D scanner fixed on a tripod with EinScan Pro 2X Color Pack (texture scans), EinTurntable (alignment based on features), and EXScan Pro 3.2.0.2 software. The number of turntable steps was varied and chosen depending on the specimen. The models were turned into meshes using the Watertight Model and High Detail presets. Pictures of the models were later generated in Meshlab (Cignoni et al., 2008) with usage of the Radiance Scaling and the Lattice shaders.

TABLE 1.	The fossil	material	collected	from	Kocury.
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Number	Taxon	Description	Notes	Figure
	Termatosaurus albertii Meyer and Plieninger, 1844	Tooth	Mentioned by Roemer (1870)	
GPIM UH No. 252	Velocipes guerichi Huene, 1932	Fibula (left)	Proximal portion	Fig. 4
ZPAL V.66/1	Kocurypelta silvestris gen. et sp. nov.	Paramedian osteoderm	Lateral portion	Fig. 7A
ZPAL V.66/2	Kocurypelta silvestris gen. et sp. nov.	Dorsal lateral osteoderm	Spike broken	Fig. 7D, Supplementary Information
ZPAL V.66/3	Archosauria indet.	Centrum of vertebra	Poorly preserved	Fig. 8D
ZPAL V.66/4	Kocurypelta silvestris gen. et sp. nov.	Maxilla (left)	Holotype	Fig. 5, Supplementary Information
ZPAL V.66/5	cf. Metaceratodus sp.	Lower dental plate (right)		Fig. 2
ZPAL V.66/6	Kocurypelta silvestris gen. et sp. nov.	Dorsal lateral osteoderm	Fragment	Fig. 7C
ZPAL V.66/7	Archosauria indet.	Skull bone (?nasal)	Fragment	Fig. 8A, B
ZPAL V.66/9	Proterochersis cf. porebensis	Carapace	Fragment	
ZPAL V.66/10	Proterochersis cf. porebensis	Bridge (right)	Fragment	Fig. 3B–D
ZPAL V.66/11	Proterochersis cf. porebensis	Carapace	Fragment	0
ZPAL V.66/12	Proterochersis cf. porebensis	Femur (right)	Fragment	
ZPAL V.66/14	Proterochersis cf. porebensis	Shell	Fragment	
ZPAL V.66/15	Proterochersis cf. porebensis	Costal	Fragment	
ZPAL V.66/16	Proterochersis cf. porebensis	Plastron	Fragment	
ZPAL V.66/18	Proterochersis cf. porebensis	Carapace (right)	Posterior portion	Fig. 3A
ZPAL V.66/19	Kocurypelta silvestris gen. et sp. nov.	Thoracic osteoderm	Lateral portion	Fig. 7B
ZPAL V.66/20	Proterochersis cf. porebensis	Pubis (left)	-	Fig. 3E
ZPAL V.66/21	Proterochersis cf. porebensis	Shell (carapace?)	Fragment	0
ZPAL V.66/25	Proterochersis cf. porebensis	Shell	Fragment	
ZPAL V.66/32	Archosauria indet.	Neural spine	Dorsal portion	Fig. 8C
ZPAL V.66/34	Proterochersis cf. porebensis	Costal	Fragment	0
ZPAL V.66/35	Proterochersis cf. porebensis	Shell	Fragment	
ZPAL V.66/37	Proterochersis cf. porebensis	Plastron (?hypoplastron)	Fragment	
ZPAL V.66/39	Archosauromorpha indet.	Tooth	2	Fig. 8E
ZPAL V.66/40	Archosauromorpha indet.	Tooth		Fig. 8F

#### SYSTEMATIC PALEONTOLOGY

DIPNOI Müller, 1844 CERATODONTOIDEI Nikolski, 1954 cf. *METACERATODUS* sp. (Fig. 2)

**Material**-ZPAL V.66/5, right lower dental plate with attached portion of the prearticular bone (Fig. 2).

**Description**—The dental plate bears four ridges. They originate medially from the mediolingual junction, located on the level of the second ridge. The junction is indistinct because of the blunt angle (140°) between the labial and medial margins, and their curvature. The medial margin of the plate is longer than lingual about 1.2 times (all measurements follow Pawlak et al. 2020). Occlusal ridges are robust. The first one is very elongated compared with other ridges, and curved labially



FIGURE 2. cf. *Metaceratodus* sp., ZPAL V.66/5 from the Upper Triassic of Kocury, Poland. Right lower dental plate in **A**, dorsal and **B**, ventral views. Scale bar equals 1 cm.

along the entire length. The second and the third ridges have similar lengths, but they are about 1.5 times shorter than the first one. Both are slightly curved medially. The last ridge is about 1.1 times longer than the third one. It is inconspicuous, and curved labially at the right angle. The plate is low-crowned (its height is approximately equal to the height of the prearticular bone), but the occlusal surface is in an advanced stage of wear, which makes it difficult to determine its original topography. Despite the wear, the ridges have visibly low crests, except the last one, which seems to be flattened. Cusps are not visible on any ridge. Interridge furrows are shallow and terminate a significant distance away from the lingual margin. This results in a wide occlusal surface. Shallow occlusal pits are present.

Pulp canals of dentine are randomly distributed on the entire occlusal side of the plate. The labial slope of the ridge is gentle, as well as that on the interridge furrows. The preserved portion of the prearticular bone has a deep double sulcus. The anterior portion of the sulcus is smaller and shallower than the posterior. The Ruge's ridge is located under the cleft between the first and second ridges. The tooth plate has no symphyseal junction, thus the lower plates were not contiguous.

Four ridges in the lower dental plates are a feature limited to ceratodontid lungfishes (Kemp, 1997a; Skrzycki, 2015). Double prearticular sulcus points to the affinity of this specimen with the genera *Ferganoceratodus*, *Metaceratodus*, or *Ptychoceratodus* (see Kemp, 1997b; Cione and Gouiric-Cavalli, 2012; Skrzycki, 2015).

**Remarks**—The most common lungfish genus in the Late Triassic of the Central European Basin was Ptychoceratodus (see Skrzycki et al., 2018). It has high-crowned dental plates with acute and slender ridges originating anteriorly, adapted to cutting rather than crushing (Skrzycki, 2015). The medial margin is usually significantly shorter than the labial, and the inner angle usually approaches 100–120° and does not exceed 130° (Skrzycki, 2015). All well-referred Ferganoceratodus species from the Triassic and Jurassic periods of Asia have dental plates generally similar to Ptychoceratodus (see Cavin et al., 2007). The type species Ptychoceratodus serratus Agassiz, 1838 (Ladinian, Germany, and Switzerland) and Ferganoceratodus jurassicus Nessov and Kaznyshkin, 1985 (Callovian, Uzbekistan) have, respectively, five to six, and four ridges in the lower dental plates, and a very conspicuous angle (139°) between lingual and medial margins (Cavin et al., 2007; Skrzycki, 2015). All these general features are inconsistent with the morphology of ZPALV.66/5.

Lower dental plates of Metaceratodus spp. have several features in common with ZPALV.66/5, i.e., medial origin of ridges, very obtuse inner angle (about 140°), and the medial margin equal or longer than the lingual (Kemp, 1997b; Cione and Gouric-Cavalli, 2012). These features of ZPAL V.66/5 resemble the type species Metaceratodus wollastoni Chapman, 1914, more than Pt. serratus and F. jurassicus. However, M. wollastoni has five ridges in lower dental plates (Kemp, 1997b). Particular similarity exists between ZPAL V.66/5, M. wichmanni Apesteguía, Agnolín and Claeson, 2007, and M. kaopen Apesteguía, Agnolín and Claeson, 2007, because all these taxa have four ridges in the lower dental plates, significantly elongated medial margins, and barely distinguishable inner angle (Cione and Gouric-Cavalli, 2012). Some specimens of *M. wichmanni* have small fifth ridge, predominantly as a characteristic heel in the posterior part of the plate (Cione and Gouric-Cavalli, 2012). Similar but inconspicuous heel is also present in ZPAL V.66/5.

There are three known dipnoan species from the Silesian Upper Triassic: *Ptychoceratodus roemeri* Skrzycki, 2015 from Krasiejów, *Ptychoceratodus silesiacus* Roemer, 1870 from Lisów, and an undescribed species of a lungfish with *Ptychoceratodus*-like dental plates from the Lisowice and Poreba localities, all having lower dental plates with four ridges which originate anteriorly. This is a distinct difference between them and ZPAL V.66/5. Moreover, the following features differentiate the lower dental plates of *Pt. roemeri* and ZPAL V.66/5: inner angle smaller than ca. 120° (except one specimen), conspicuous tip of the inner angle, and medial margin significantly shorter than lingual. All these features can be also used to distinguish ZPAL V.66/5 and lower dental plates of *Ptychoceratodus silesiacus*, and the lungfish from Lisowice and Poreba. However, two larger specimens from Lisowice have a significantly elongated first ridge. This results in the medial to lingual margin length ratio similar to that of ZPAL V.66/5. Determination of the taxonomic affinities of the lungfish from Kocury should be treated with caution as there is only one collected specimen from there, and a wide intraspecific variability is known for dipnoan dental plates.

# TESTUDINATA Klein, 1760 PROTEROCHERSIDAE Nopcsa, 1923 *PROTEROCHERSIS* Fraas, 1913b *PROTEROCHERSIS* cf. *POREBENSIS* Szczygielski and Sulej, 2016 (Fig. 3)

**Material**–ZPAL V.66/9, carapace fragment; ZPAL V.66/10, bridge fragment; ZPAL V.66/11, carapace fragment; ZPAL V.66/12, part of a right femur; ZPAL V.66/14, shell fragment; ZPAL V.66/15, costal fragment; ZPAL V.66/16, plastron fragment; ZPAL V.66/18, posterior right part of the carapace; ZPAL V.66/20, left pubis; ZPAL V.66/21, shell (?carapace) fragment; ZPAL V.66/25, shell fragment; ZPAL V.66/34, costal fragment; ZPAL V.66/35, shell fragment; ZPAL V.66/37, plastron (? hyoplastron) fragment.

**Description**—The most diagnostic specimen (ZPAL V.66/18; Fig. 3A) represents the posterior right part of the carapace of a middle-sized individual (slightly larger than ZPAL V.39/48 but smaller than ZPAL V.39/72, estimated carapace length about 43 cm; see Szczygielski et al., 2018) and exhibits morphology typical for Proterochersidae. It consists of the nearly complete areas of the last (probably 14th) and second-to-last (13th) marginal, and partial areas of the third-to-last (12th) marginal (along most of the sulcus with the succeeding marginal) and the last (fifth) vertebral scute (posterolateral corner). The caudal notch (sensu Gaffney, 1990; Szczygielski and Sulej 2016; Szczygielski et al., 2018) is partially preserved, missing the diagnostic midsection, therefore its complete shape is unknown. However, the inclination of the preserved lateral portion is consistent with the morphologies observed in triangular notches of Proterochersis porebensis Szczygielski and Sulej, 2016, and different from the rounded notches of at least some Pr. robusta Fraas, 1913b, specimens (most notably, SMNS 17561, less so CSMM uncat.; compare Szczygielski and Sulej, 2016; Szczygielski et al., 2018). The last marginal is pronounced but rounded (lacking a sharpened tip present in some large specimens of Pr. porebensis - see Szczygielski et al., 2018), the external surfaces of the last vertebral and second-to-last marginal bear striations, and the vertebromarginal sulcus is clearly undulating, indicative of postjuvenile, possibly adult ontogenetic stage (Szczygielski et al., 2018). The visceral surface of the specimen is partially destroyed; no remains of ilia or a sacrum are preserved. No sutures are visible, the fragment is completely ankylosed.

The presence of a clear caudal notch, the shape of the posteriormost marginals, the layout of scute sulci, and the typical features of the scute surfaces (striation, undulating edges) refute its attribution to most well-known Triassic turtles (Gaffney, 1990; Rougier et al., 1995; Sterli et al., 2007, 2020; Joyce et al., 2009; Szczygielski and Sulej, 2019) and enable its identification as a member of Proterochersidae (Szczygielski and Sulej, 2016, 2019; Szczygielski et al., 2018). Given the fragmentary nature of this specimen, its specific identity is, unfortunately, uncertain.



FIGURE 3. *Proterochersis* cf. *porebensis* Szczygielski and Sulej, 2016, from the Upper Triassic of Kocury, Poland. **A**, ZPALV.66/18, posterior right part of the carapace in dorsal view; **B**–**D**, ZPALV.66/10, right bridge fragment in **B**, ventral, **C**, dorsal and **D**, lateral views; **E**, ZPALV. 66/20, left pubis in anterior view. The position of the specimens is indicated in gray within the outlines of complete carapace in dorsal (top) and ventral (middle) views, and pelvis (bottom). Sulci in **B** and **D** indicated by the dotted lines. Scale bar equals 1 cm; **C** not to scale.

The only Triassic turtle known thus far from that part of the Germanic Basin is Proterochersis porebensis, with its type locality (Poreba) placed slightly over 70 km to the south-east from Kocury (Sulej et al., 2012; Niedźwiedzki et al., 2014; Zatoń et al., 2015; Szczygielski and Sulej, 2016; Bajdek et al., 2019). Since the morphology of the Kocury specimen ZPAL V.66/18 is indistinguishable from the known specimens of *Pr. porebensis*, including the partially preserved caudal notch (Szczygielski and Sulej, 2016, 2019; Szczygielski et al., 2018), it seems most parsimonious that it is a representative of the same species rather than the German proterochersids Pr. robusta or Keuperotesta limendorsa Szczygielski and Sulej, 2016, or a new taxon altogether. On the other hand, the most diagnostic, medial part of the caudal notch is not preserved and its shape can be only assumed based on the inclination of the preserved portion. For that reason, we identify the turtle from Kocury as Proterochersis cf. porebensis.

The specimens ZPAL V.66/9, 11, 14, 15, 16, 21, 25, 33, 34, 35, and 37 represent smaller shell fragments, and do not present diagnostic features allowing their identification other than as an indeterminate turtle. Among them, ZPAL V.66/9 and 11 have the striation and sinuous sulci typical for the circum- and interpleural or circumsupramarginal sulci of Proterochersis spp. (Szczygielski et al., 2018). ZPAL V.66/15 has its external surface poorly preserved but its cross-section with a gentle visceral bulge and probably sinuous transverse sulcus suggest its interpretation as a costal fragment. ZPAL V.66/34 lacks sulci, but also shows a bulge characteristic to costals and subtle transverse growth marks on its external surface (compare with Szczygielski et al., 2018). ZPAL V.66/14 shows a non-sinuous, gently bowed sulcus with one elevated edge, suggesting its interpretation as either a part of the plastron or a fragment of the vertebral or marginal part of the carapace (compare with Szczygielski et al., 2018). ZPAL V.66/16 exhibits a partially preserved pronounced ridge on one of its surfaces comparable to the posterior process of the entoplastron (see Szczygielski and Sulej, 2016, 2019) and ZPAL V.66/37 has one of its edges worn, but seemingly natural (as evidenced by the remnants of the cortex) and gently concave - both may thus be interpreted as parts of the anterior plastral lobe. ZPAL V.66/21 has an irregular outline that suggests its interpretation as either a dermal element of the carapace (compare Szczygielski and Sulej, 2019) or a fragment of a skull of an indeterminate reptile – a rugose, turtle-like relief on the external surface and much smoother visceral surface favor the former interpretation. A rugose turtle-like external texture is also exhibited by ZPALV.66/35. ZPALV.66/34 presents a smoother and more striated surface that also fits within the spectrum of textures observed in Proterochersis spp. (Szczygielski et al., 2018; Szczygielski and Sulej, 2019; Szczygielski, pers. obs. 2020). The attribution of these fragmentary specimens to Proterochersis cf. porebensis is tentative, but at this time seems the most probable.

ZPALV.66/10 is a right bridge fragment, consisting of the areas of the posterior part of the sixth marginal, most of the seventh marginal, and minute fragments of the adjacent supramarginals and plastron (Fig. 3B–D). The morphology and sulci layout are consistent with that described for *Proterochersis* spp. (Szczygielski and Sulej, 2016, 2019; Szczygielski et al., 2018). Additionally, a costoperipheral suture is partially visible at the level of the marginosupramarginal sulcus (Fig. 3C), as in *Proterochersis porebensis* but lower than in *Proterochersis robusta* (see Szczygielski and Sulej, 2019).

ZPAL V.66/20 is identifiable as an isolated, partial left turtle pubis (Fig. 3E). The lateral pubic process is nearly complete, flat in its dorsal part, with sharpened medial/craniomedial edge, and in ventral part expanded predominantly craniocaudally into a roughly tear-shaped point of attachment with the plastron. The articular area is mostly damaged, with only small parts of

natural bone surface preserved. This surface is wavy to rugose, resembling unfinished (incompletely ossified) bone with a cartilaginous finish. This, together with the size of the specimen, suggests a relatively young ontogenetic stage of the individual. Dorsally, the pubis is broken below the acetabulum. Likewise, most of the pubic plate is missing, including the anterior edge of the notch between the lateral pubic process and the epipubis, but the lateral part of the conspicuous edge of the pelvic fossa encircled by the pubes and ischia is preserved and the anterior edge of the obturator foramen is identifiable. The observed morphology is consistent with Triassic turtles (Gaffney, 1990; Sterli et al., 2007, 2020; Joyce et al., 2013) and Proterochersis spp. in particular (Szczygielski and Sulej, 2016, 2019). The only possible difference is the sharp craniomedial edge of the lateral pubic process-such a morphology is not visible in the specimens of Proterochersis porebensis discovered thus far (Szczygielski, pers. obs. 2020). However, this may be an effect of their incomplete preparation, intraspecific or ontogenetic variability, or taphonomy.

ZPAL V.66/12 is a partial shaft of a long bone we identify as a shaft of the right femur of a turtle given its size, gentle constriction, cross-section (triangular at one-supposedly proximaland oval at the other-supposedly distal-end), flat supposed ventral and rounded supposed dorsal surface, presence of two gentle condyles comparable to the condyles at the base of the major (lower) and minor (higher) trochanters and a longitudinal ridge extending distally from the former condyle. Taking into account the incompleteness of that specimen, this identification must be treated with caution, but the specimen is nearly identical with a large, yet undescribed femur of *Proterochersis porebensis* found in Poręba (ZPAL V.39/432; compare also with fig. 8 in Szczygielski and Sulej, 2016).

> ARCHOSAURIA Cope, 1869 DINOSAURIA Owen, 1842 THEROPODA Marsh, 1881 ? NEOTHEROPODA Bakker, 1986 VELOCIPES von Huene, 1932 VELOCIPES GUERICHI von Huene, 1932 (Fig. 4)

**Material**-GPIM UH no. 252, proximal portion of the left fibula lacking the anteroproximal and posteroproximal processes.

**Remarks**—The holotype of *Velocipes guerichi* von Huene, 1932, an incomplete left fibula (GPIM UH No. 252; Fig. 4), was the first bone collected from the Kocury locality in the 19th Century (von Huene, 1932; Skawiński et al., 2017). It was considered to be a 'coelurosaurian' or halticosaurid theropod (von Huene, 1932, 1956), podekosaurid (Carroll, 1988), a neotheropod congeneric with *Liliensternus* (Welles, 1984), an indeterminate ceratosaurian (Tykoski and Rowe, 2004; Weishampel et al., 2004), or an indeterminate vertebrate (Rauhut and Hungerbühler, 1998). The specimen was recently rediscovered in the collection of the Geological-Palaeontological Institute and Museum of the University of Hamburg and redescribed as a neotheropod dinosaur (for detailed description and comparisons of the specimen see Skawiński et al., 2017).

The preserved portion of the bone is 164 mm long. The bone is medially concave in proximal view. It is asymmetrical in lateral view with a nearly straight anterior margin and proximally concave posterior one, closely resembling fibulae of the basal neotheropods, *Dilophosaurus wetherilli* Welles, 1954 (see Marsh and Rowe, 2020), *Liliensternus liliensterni* von Huene, 1934 and *Dracoraptor hanigani* Martill, Vidovic, Howells and Nudds, 2016. On the medial side of the specimen there is a prominent longitudinal fossa, that is observed only in neotheropods



FIGURE 4. *Velocipes guerichi* von Huene, 1932, from the Upper Triassic of Kocury, Poland. GPIM UH no. 252, proximal portion of the left fibula in **A**, lateral and **B**, medial views. The position of the specimen is indicated in gray within the outlines of a complete fibula. Scale bar equals 2 cm.

(Nesbitt, 2011); however, a shallower fossa occurs also in early sauropodomorphs such as *Buriolestes schultzi* Cabreira, Kellner, Dias-da-Silva, da Silva, Bronzati, de Almeida Marsola, Müller, de Souza Bittencourt, Batista, Raugust, Carrilho, Brodt and Langer, 2016 (see Müller et al., 2018). Medially, there is a small rugosity located near the anterior border of the bone, that plausibly was related to the fibular crest of the tibia. The relatively large tubercle for the m. iliofibularis visible in lateral view may be a diagnostic feature of *V. guerichi*; however, it displays quite wide intraspecific variation within theropods (Skawiński et al., 2017). A similar condition is also present in the early sauropodomorph *Buriolestes schultzi* (see Müller et al., 2018).

# ARCHOSAURIA Cope, 1869 AETOSAURIA Marsh, 1884 (sensu Parker, 2007) STAGONOLEPIDIDAE Lydekker, 1887 (sensu Heckert and Lucas, 2000) TYPOTHORACINAE Parker, 2007 (sensu Parker, 2016) PARATYPOTHORACINI Parker, 2007 KOCURYPELTA, gen. nov.

Type Species-Kocurypelta silvestris, sp. nov.

**Diagnosis**—As for the type species.

**Etymology** – The generic name is derived from Kocury village, where the material was collected, and the Greek term  $\pi \epsilon \lambda \tau \eta$  (*péltē*) meaning 'the shield'.

KOCURYPELTA SILVESTRIS, sp. nov. (Figs. 5–7)

**Holotype**-ZPALV.66/4, left maxilla lacking the anteriormost portion.

**Referred Material**–ZPAL V.66/1, isolated left paramedian dorsal osteoderm; ZPAL V.66/2, isolated right dorsal lateral osteoderm; ZPAL V.66/6, part of isolated right dorsal lateral osteoderm; ZPAL V.66/19, part of isolated broken ventral thoracic or paramedian osteoderm.

**Type Locality**–Kocury near Dobrodzień, southern Poland (Fig. 1). Geographic coordinates: 50°46′53.0′′N, 18°26′39.0′′E.

**Type Horizon**—Patoka Member of the Grabowa Formation, Upper Triassic.

**Diagnosis**—An aetosaur with the following unique combination of features: maxilla with a long posterior edentulous portion (longer than 80% of the posterior maxillary process; autapomorphy); position of the medial shelf restricted to the posterior portion of the maxilla, ventral to the antorbital fenestra (autapomorphy); maxillary accessory cavity (sensu Witmer, 1997) not roofed by the medial ridge of the ascending process anteriorly (autapomorphy); maxilla in medial view lacking the distinct choanal recess anterior to the ascending process (autapomorphy).

If the osteoderms represent the same species as the maxilla, then this taxon can be further diagnosed by the following combination of features: dorsal trunk paramedian osteoderms greatly expanded mediolaterally, with width to length ratio of the widest trunk paramedian osteoderms probably greater than 3.5 (shared with Apachesuchus heckerti, Paratypothorax andressorum. Redondasuchus rineharti. Rioarribasuchus chamaensis, Tecovasuchus chatterjeei and *Typothorax* coccinarum); dorsal trunk paramedian osteoderms with radial ornamentation consisting of very long rays (longer than 50% of the plate at the lateral side), and paralleling the posterior margin of the plate (shared with *Pa. andressorum*); posterior margin of the dorsal trunk paramedian osteoderms thickened and 'beveled' in relation to the anterior and the ornamented mid-portion (shared with Te. chatterjeei); lateral trunk osteoderms with dorsoventrally flattened spikes (shared with Pa. andressorum); lateral trunk osteoderms with not defined anterior bar (shared with Pa. andressorum, different from Te. chatterjeei).

The new taxon is assigned here to Typothoracinae (sensu Parker, 2016) based on the presumed width to length ratio of the widest paramedian osteoderms (rows 9–11) in the dorsal trunk series greater than 3.5. The new taxon belongs to Paratypothoracini (sensu Parker, 2007) based on the presence of a dorsoventrally flattened spike on anterior dorsal lateral osteoderm.

The new taxon differs from *Pa. andressorum* in that the maxilla of *Kocurypelta silvestris*: (1) has an elongated posterior portion lacking the tooth alveoli; (2) has the contact of the ascending process with the lacrimal bone restricted to its posterodorsal corner; (3) lacks a finger-like downcurved posterior process of the maxilla; (4) lacks a distinct crest and transverse ridge of the antorbital fossa.

If the osteoderms represent the same taxon as the maxilla, it can be further differentiated from *Pa. andressorum* by: (5) the dorsal trunk paramedian plate having its posterior margin welldefined, thickened, and 'beveling' in relation to the anterior and mid-portion; and (6) the anterior dorsal lateral trunk osteoderms lacking a tongue-shaped process at the dorsal flange.



FIGURE 5. Kocurypelta silvestris gen. et sp. nov. from the Upper Triassic of Kocury, Poland. The holotype specimen ZPALV.66/4, posterior half of the left maxilla in **A**, lateral, **B**, ventral and **C**, medial views. Eroded surface on the medial side (**C**) is indicated by the dashed line. Scale bar equals 2 cm.

**Etymology**—The specific name refers to the Kocury forest, where the excavations took place, and honors the local authorities who helped in organization of the excavations. The whole name means 'the forest shield from Kocury'.

**Remarks**—Given that all the material referred here to *Kocurypelta silvestris* was collected as isolated bones from the conglomerate, it most likely does not belong to a single individual. Expecting that osteoderms of similar morphology may occur in different aetosaur genera, we decided to establish *Kocurypelta silvestris* gen. et sp. nov. based on the maxilla that we believe is more taxonomically informative. The osteoderms and maxilla are of proportionally corresponding sizes, hence the most parsimonious assumption is that they belong to the same species. Nevertheless, being aware that the material currently known is scarce and incomplete, more material is needed to support or refute this taxonomic statement.

# Description

**Maxilla**—The maxilla of *Kocurypelta silvestris* ZPAL V.66/4 (Fig. 5) is low and anteroposteriorly elongated, with a straight ventral margin. It forms the anterior, anterodorsal, and ventral margin of the antorbital fenestra. The anteriormost portion of

the maxilla is not preserved, therefore the contribution of the maxilla to the externals nares is not clear. The posterior process has a small dorsal tongue, revealing a complex nature of the contact with the jugal. This complex intersection is a synapomorphy of the clade Aetosauria + the non-aetosaur Revueltosaurus callenderi Hunt, 1989 (see Nesbitt, 2011). The posteriormost portion of the bone expands dorsoventrally, such as in, e.g., aetosaurs and Revueltosaurus (see Nesbitt, 2011). Measured from the rostral border of the antorbital fenestra, the process is 72 mm long. The posteroventral tongue of the posterior maxillary process is short. No buccal emargination is present and the tooth alveoli are nearly flush with the lateral side of the maxilla. The maxilla of K. silvestris seems to be relatively large in size compared with other aetosaurs (Fig. 6), similar as in large specimens of Stagonolepis spp. and Desmatosuchus smalli (see Small, 2002; Sulej, 2010).

The ascending process is mediolaterally thickened in dorsal view. The contact with the nasal in ZPAL V.66/4 seems to be oblique, descending anteriorly at an angle of 45° in relation to the tooth row that suggest presence of a well-developed descending process of the nasal. Similar conditions are present in the maxillae of *Aetosauroides scagliai* Casamiquela, 1960 (UFSM 11505), *Stagonolepis robertsoni* Agassiz, 1844 and



FIGURE 6. Comparison of the maxillae morphology among Aetosauria. Scale bar equals 5 cm.

Sta. olenkae Sulej, 2010 (see Walker, 1961; Sulej, 2010; Biacchi Brust et al., 2018). In Aetosaurus ferratus Fraas, 1877, Paratypothorax and ressorum Long and Ballew, 1985 (SMNS 19003), and Stenomyti huangae Small and Martz, 2013 the descending process of the nasal is less prominent and forms an almost straight angle with the posterior process of the maxilla (Schoch, 2007; Small and Martz, 2013; Schoch and Desojo, 2016). In Neoaetosauroides engaeus Bonaparte, 1969, Longosuchus meadei Hunt and Lucas, 1990, and Desmatosuchus spurensis Case, 1920 the descending process of the nasal is relatively reduced and the suture with the nasal is almost straight in lateral view (Case, 1921; Small, 2002; Parrish, 1994; Desojo and Báez, 2007). Contact with the lacrimal of the ascending process of the maxilla in K. silvestris seems to be reduced when compared with other aetosaurs (e.g., Stenomyti huangae, Paratypothorax and ressorum, Stagonolepis spp.). The dorsal process of maxilla tapers posterodorsally, differently than in other aetosaurs, in which it maintains a relatively constant dorsoventral height (Nesbitt, 2011). However, it is possible, that the process is not completely preserved in ZPAL V.66/4. The suture with the lacrimal, although difficult to trace in ZPAL V.66/4, seems to be somewhat oblique dorsoventrally in medial view. The groove along the medial surface of the ascending process is very weakly developed in K. silvestris, trending along the anterior margin of the process.

The antorbital fossa is well-demarcated, although relatively shallow, especially in its ventral portion. Anterodorsally, it nearly reaches the contact with the nasal, similar to *Sta. robertsoni*, *Sta. olenkae*, *A. scagliai*, *A. ferratus*, *Pa. andressorum*, *Ste. huangae*, and *Calyptosuchus wellesi* Long and Ballew, 1985 (UCMP 195193). However, the whole ascending process of *K. silvestris* seems to be slightly shorter in comparison with these taxa (Walker, 1961; Schoch, 2007; Sulej, 2010; Schoch and Desojo, 2016; Biacchi Brust et al., 2018; Parker, 2018). In contrast, the antorbital fossa of *Desmatosuchus smalli* Parker, 2005, *D. spurensis*, and *L. meadei* is very narrow dorsoventrally (Case, 1922; Small, 2002; Parker, 2005).

There is no prominent transverse ridge bordering the antorbital fossa on the lateral surface in *K. silvestris*, in contrast to the distinct ridge present in *A. scagliai, Ste. huangae, Pa. andressorum, Sta. robertsoni, Sta. olenkae*, and *C. wellesi* (see Walker, 1961; Sulej, 2010; Small and Martz, 2013; Schoch and Desojo, 2016; Biacchi Brust et al., 2018; Parker, 2018). The condition of *K. silvestris* is similar to that of *D. spurensis, D. smalli*, and *L. meadei* in which the ridge is extremely weak or absent (Case, 1922; Parrish, 1994; Small, 2002). Lack of a distinct ridge in ZPAL V.66/4 may be a result of erosion during its deposition in the high-energy environment of the Kocury locality, although, a number of specimens collected from there preserved even more delicate aspects of anatomy and no abraded surface is



FIGURE 7. Kocurypelta silvestris gen. et sp. nov. osteoderms from the Upper Triassic of Kocury, Poland. **A**, ZPAL V.66/1, left paramedian dorsal osteoderm in dorsal view; the position of the specimen is indicated in gray within the outline of a complete osteoderm; **B**, ZPAL V.66/19, a ventral thoracic or paramedian osteoderm; **C**, ZPAL V.66/6, a partial right dorsal lateral osteoderm in dorsal view; **D**, ZPAL V.66/2, a right anterior dorsal lateral osteoderm in lateral view. Scale bar equals 1 cm.

visible in this region of ZPAL V.66/4. Additionally, there is no trace of a longitudinal crest on the lateral surface of the caudal portion of the posterior process, near the contact with the jugal, even though the lateral side of the posterior process is rather well-preserved. In contrast, *Sta. olenkae* and other aetosaurs (e.g., *Ste. huangae, A. ferratus, A. scagliai*) seem to always have a distinct longitudinal crest (Schoch, 2007; Sulej, 2010; Small and Martz, 2013) that impacts the shape of the bone in the caudoventral area of the posterior process, making the central portion of the posterior process. This is not the case in ZPAL V.66/4, in which the caudal portion of the posterior process is smooth laterally.

On the medial surface of K. silvestris there is a medial shelf located ventral to the antorbital fenestra. Its mediolateral width is similar to that of Sta. olenkae ZPAL AbIII/2151/3. However, the anterior portion of the shelf does not contribute to the medial surface of the ascending process in K. silvestris, being restricted to the posterior portion of the bone. The medial ridge of the ascending process is roofing the anterior cavity (pneumatic accessory cavity sensu Witmer, 1997) in Sta. olenkae (see Sulej, 2010). It is not the case in ZPAL V.66/4, in which there is no ridge on the medial wall of the ascending process. The palatal processes of the maxilla are poorly preserved in the K. silvestris holotype. Anteriorly, the medial wall of the ascending process of the maxilla is flat and eroded in ZPAL V.66/4, with no preserved trace for the palatal process of the premaxilla (Fig. 5C). In Sta. olenkae or D. smalli there is a concavity for the anterior medial maxillary fossa present (Small, 2002; Sulej, 2010). It implies lack of a distinct choanal recess (sensu Witmer, 1997) in *K. silvestris* because the medial shelf is not present on the anterior portion of the maxilla. The medial shelf of *K. silvestris* is located exclusively ventral to the antorbital fenestra, where it contacts the palatine, in contrast to the state observed in *Sta. olenkae* (ZPAL AbIII/1997), *Sta. robertsoni* (NHMUK PV R4787) or in other aetosaurs (Small and Martz, 2013), in which it extends beyond the anterior edge of the antorbital fenestra.

Five alveoli are preserved in ZPAL V.66/4 and taking into consideration that the average number of maxillary teeth in aetosaurs is ten, about 30% of the anterior portion of the maxilla is missing. On the other hand, the very low number of preserved tooth sockets suggest that it could be much more anteriorly expanded, like in *D. smalli, D. spurensis*, or *L. meadei* (see Case, 1922; Parrish, 1994; Small, 2002; Parker, 2005). Interdental plates are separated in medial view in *K. silvestris*, as in other aetosaurs and nearly all archosauriforms with the exception of rauisuchids and some theropod dinosaurs (Nesbitt, 2011; Marsh and Rowe, 2020). Spaces between the alveoli are greater than in *Stagonolepis* spp. or *Pa. andressorum*.

In Kocurypelta silvestris there are only two alveoli caudal to the anterior margin of the antorbital fossa, with only one located posterior to the anterior margin of the antorbital fenestra. In other aetosaurs, the number of the posterior alveoli is greater; there are at least three in Aetosauroides scagliai, Aetosaurus ferratus, and Ste. huangae (see Walker, 1961; Small and Martz, 2013; Biacchi Brust et al., 2018). In Sta. olenkae there are five (ZPAL AbIII/576) to six (ZPAL AbIII/574, 1997, 2151/3) alveoli caudal to the anterior margin of the antorbital fossa, including three (ZPAL AbIII/576), four (ZPAL AbIII/ 2151/3, 1997), or five (ZPAL AbIII/574) located caudally to the anterior margin of the antorbital fenestra. There are eight teeth at the first two-thirds of the maxilla length in N. engaeus (see Desojo and Báez, 2007), although it is not clear to what degree the posterior portion is edentulous. Among Typothoracinae, there are five caudal alveoli in Pa. and ressorum SMNS 19003 (Schoch and Desojo, 2016). Among Desmatosuchinae, three alveoli are located caudally in L. meadei TMM 31185-84B (Parrish, 1994) and D. haplocerus TTUP 9024 (Small, 2002). Based on the varied distribution of the number of alveoli in similar-sized specimens of Sta. olenkae, it seems that it has little correlation with ontogeny. In K. silvestris the posterior edentulous portion is especially long, measuring 63 mm, that is 87.5% of the posterior maxillary process length (measured from the anterior border of the antorbital fenestra). In medial view the posterior process bends distinctly laterocaudally (Fig. 5C).

Dentition in the posterior half of the maxilla is usually present in Archosauria. Among Triassic archosaurs, the long edentulous posterior portion of the maxilla was described only in Erpetosuchidae (Nesbitt, 2011). In the erpetosuchid Parringtonia gracilis Huene, 1939 three of a total of five alveoli are located caudally to the antorbital fossa (Nesbitt and Butler, 2012). Only the last alveolus is located in the line with the anterior border of the antorbital fenestra. That condition is similar to that seen in K. silvestris. However, in Parringtonia gracilis the depth of the antorbital fossa is greater, the transverse ridge is more prominent and trends along the whole length of the antorbital fossa, the medial wall of the antorbital fossa is longer, the medial ridge trends anteriorly of the fossa, and the height to width ratio of the posterior process is smaller than in K. silvestris. In Erpetosuchus granti Newton, 1894 the maxilla is distinctly wider than high in the posterior portion, and teeth are located more medially. Contact with the jugal is simpler and broader than in K. silvestris (see Benton and Walker, 2002) compared with E. granti. Also, the teeth in E. granti are located on an alveolar platform formed by a dorsoventrally thickened maxilla. The antorbital fossa is not recessed in any point of the maxilla of K. silvestris, in contrast to Parringtonia gracilis and E. granti (see Nesbitt and Butler, 2012). An edentulous posterior portion of the maxilla was described also in the erpetosuchid Pagosvenator candelariensis Lacerda, De França and Schultz, 2018. It differs from K. silvestris in a slit-like antorbital fenestra, posteriorly projecting ascending process of the maxilla, and the great anterior expansion of the antorbital fossa. In Pagosvenator candelariensis at least six teeth were present, five of them located posterior to the anterior margin of the antorbital fossa and two of them located posteriorly to the anterior border of the antorbital fenestra (Lacerda et al., 2018).

The mediolateral width of the posterior process of the ZPAL V.66/4 is slightly greater than the dorsoventral height of this process, similar to *Sta. robertsoni, Effigia okeeffeae* Nesbitt and Norell, 2006, *Lotosaurus adentus* Zhang, 1975; however, not in the same ratio as in *Erpetosuchus granti* and *Parringtonia gracilis* (see Walker, 1961; Nesbitt, 2011; Nesbitt and Butler, 2012).

**Trunk Paramedian Osteoderm**—A single specimen of a left dorsal trunk paramedian osteoderm, ZPAL V.66/1, has been recovered (Fig. 7A). It lacks most of the medial part including the dorsal eminence. The specimen is encased in rock matrix and only its dorsal side is exposed. The osteoderm is narrow and lateromedially elongated in a manner similar to *Paratypothorax andressorum* and *Typothorax coccinarum* (e.g., Martz, 2002; Desojo et al., 2013; Schoch and Desojo, 2016). Based on the ornamentation arrangement and comparing with other aetosaurs, such as *Pa. andressorum* or *Tecovasuchus chatterjeei* (see Lucas et al. 2006; Martz and Small 2006), it seems that it is broken close to the dorsal eminence and there is no ventral flexure at the center of ossification, characteristic for Paratypothoracini (Parker, 2007). Ornamentation on the dorsal surface of ZPAL V.66/1 is radial and consists of very long rays paralleling the posterior margin of the plate as in *Pa. andressorum*; it is especially similar to the paramedian osteoderms of PEFO 3004 (Long and Ballew, 1985; Hunt and Lucas, 1992; Long and Murry, 1995; Lucas et al., 1995, 2006; Heckert and Lucas, 2000; Parker, 2007; Desojo et al., 2013; Schoch and Desojo, 2016).

The anterior bar of ZPALV.66/1 is narrower in comparison to Pa. andressorum specimens PEFO 3004, SMNS 5721, and Te. chatterjeei (TTUP 545, 9222 and UMNP 9600; see: Long and Ballew, 1985; Hunt and Lucas, 1992; Lucas et al., 1995, 2006; Martz and Small, 2006; Schoch and Desojo, 2016). However, the shape and ornamentation of the plates can differ depending on the position on the trunk (e.g., Taborda et al., 2015), therefore the width of the anterior bar cannot be used as a feature distinguishing these taxa. Close to the lateral margin, the anterior bar starts to expand anteroposteriorly as usual in aetosaur trunk paramedian osteoderms (e.g., Long and Murry, 1995; Desojo et al., 2013). The lateral tip of the anterior bar is broken in ZPAL V.66/1. In most aetosaurs it forms a distinct process (e.g., Casamiquela, 1960; Walker, 1961; Hunt and Lucas, 1992; Lucas et al., 2002, 2006; Martz, 2002; Desojo et al., 2013; Taborda et al., 2015).

The posterior margin of the plate is thickened relative to the anterior and middle section of the osteoderm. It forms a defined, raised ridge that continues transversely across the entire preserved portion of the specimen. The area posterior to the ridge is sharp-edged and is abruptly sloped posteroventrally, giving the posterior edge of the osteoderm a beveled appearance. This structure of the posterior margin is similar as in *Te. chatterjeei* (TTUP 545, 9222, UMNP 9600), and it is considered to be one of the distinctions between *Te. chatterjeei* and *Pa. andressorum* (see Lucas et al., 1995; Martz and Small, 2006).

Lateral Osteoderms-Two specimens of right lateral osteoderms of the anterior region of the trunk (ZPAL V.66/2, Fig. 7C; and ZPAL V.66/6, Fig. 7D) were collected. ZPAL V.66/2 is almost entirely preserved, with the exception of the spike that is broken at the base. In ZPAL V.66/6 only part of the most anterior rounded portion is preserved. Overall, the specimens resemble the lateral osteoderms of Pa. and ressorum (PEFO 3004, SMNS 5721; Long and Ballew, 1985; Hunt and Lucas, 1992; Lucas et al., 2006; Schoch and Desojo, 2016). However, the dorsal flange is not tongue-shaped as in other Paratypothoracini (Long and Ballew, 1985; Hunt and Lucas, 1992; Lucas et al., 1995, 2006; Martz and Small, 2006; Parker, 2007; Schoch and Desojo, 2016). The basal part of the osteoderm ZPAL V.66/2 seems to be more circular in ventral view than the lateral osteoderms of PEFO 3004. Although the spike in ZPAL V.66/2 is not preserved, based on the dorsoventrally elongated shape of the cracked surface, we presume that it was wide and flattened, similar as in the lateral osteoderms of PEFO 3004 and SMNS 5721 (Long and Ballew, 1985; Hunt and Lucas, 1992; Lucas et al., 2006; Schoch and Desojo, 2016). The external surface of ZPAL V.66/2 and ZPAL V.66/6 has radial ornamentation. In the specimen ZPAL V/66/2 that ornamentation consists of long rays, which start from the base of the smooth spike, and continue through the margins of the plate, almost exactly like in the lateral osteoderms of Pa. and ressorum, PEFO 3004 and SMNS 5721 (Long and Ballew, 1985; Hunt and Lucas, 1992; Lucas et al., 2006; Schoch and Desojo, 2016). In both ZPAL V.66/2 and ZPAL V.66/6 the anterior bar is poorly defined, similarly as in the lateral osteoderms of Pa. and ressorum PEFO 3004, while the lateral osteoderms of Te. chatterjeei TTUP 545, UMMP 8869 have a distinct anterior bar, similar to the anterior bar on the paramedian plates of that species (Hunt and Lucas, 1992; Lucas et al., 1995, 2006 Martz and Small, 2006). Additionally,

osteoderms of *Te. chatterjeei* have a more regularly arranged ornamentation than ZPAL V.66/2 and ZPAL V.66/6, which consists of a greater number of more closely spaced radial grooves (Lucas et al., 1995; Martz and Small, 2006).

Thoracic Ventral or Trunk Paramedian Osteoderm-A single specimen of a possible thoracic ventral or a trunk paramedian osteoderm ZPAL V.66/19 (Fig. 7B) was collected. Because the specimen is broken and only the ventral side is exposed, the assignment of the specimen to the ventral or dorsal series depends on interpretation. Plausibly, about half of the osteoderm is preserved. The specimen is surrounded by rock matrix and a natural cast of the other half, destroyed during recovery, is preserved on the surface of the matrix next to the bone. The ventral surface is divided into two distinguishable areas oriented anteroposteriorly: a bigger, slightly convex area covering the anterior and a middle part of the ventral surface of the platecorresponding to the anterior bar and most of the ornamented part of the dorsal surface, and a narrow, flat area with lateromedially oriented color striations (most likely growth marks), at the posterior portion of the plate-place of contact with the anterior bar of the following osteoderm. Interpreting it as thoracic ventral osteoderm we tentatively refer it to Kocurypelta silvestris, due to its noticeably smaller size and different proportions in comparison with the trunk paramedian plate ZPAL V.66/1. The ventral thoracic osteoderms in most aetosaurs, if present, form multiple rows covering almost the entire abdomen (e.g., Walker, 1961; Schoch, 2007; Heckert et al., 2010; Desojo et al., 2013; Taborda et al., 2015; Parker, 2016). They usually are square and are considerably smaller than the dorsal paramedian ones (e.g., Walker, 1961; Schoch, 2007; Heckert et al., 2010; Desojo et al., 2013; Parker, 2018). On the other hand, ZPAL V.66/19 seems to be significantly elongated mediolaterally and rectangular, which gives the alternative interpretation that it could be a trunk paramedian osteoderm of a smaller individual of K. silvestris or of a different aetosaur taxon of smaller size, e.g., Aetosaurus ferratus (see Schoch 2007). Dorsal and ventral osteoderms from the caudal region are longer anteroposteriorly than mediolaterally, and the appendicular osteoderms do not have the anterior bar that excludes these interpretations for ZPAL V.66/19 (e.g., Walker, 1961; Schoch, 2007; Heckert et al., 2010; Parker and Martz, 2010; Desojo et al., 2013).

#### Taxonomy of the New Aetosaur

Despite the vast similarity in the morphology of the osteoderms collected from Kocury with those of *Paratypothorax andressorum* (see Long and Ballew, 1985; Lucas et al., 2006; Schoch and Desojo, 2016), we decided to establish a new aetosaur taxon, *Kocurypelta silvestris* gen. et sp. nov., on the basis of the maxillary bone with a distinctive anatomy. Due to the uncertain status of *Pa. andressorum* (e.g., Parker, 2016; Schoch and Desojo, 2016), significant differences in the maxillary anatomy of the material from Kocury, and some distinctions in osteoderms structure, we chose to erect a new genus for the latter, rather than assigning it to *Paratypothorax*.

The classification of aetosaurs is based heavily on the morphology of osteoderms (e.g., Long and Ballew, 1985; Long and Murry, 1995; Parker, 2007; Desojo et al., 2013; Parker, 2016). This is justified by several reasons, e.g., an extensive dermal armor being one of the diagnostic features for Aetosauria (see Desojo et al., 2013; Parker, 2016), and the fact that osteoderms, particularly the dorsal paramedian and the dorsal lateral ones, are the most common parts of the aetosaur skeleton that could be found in the field and unambiguously assigned to the group (Long and Ballew, 1985; Parker, 2007, 2016; Desojo et al., 2013). Moreover, the concept of using the dermal armor as a major source of characters distinguishing the aetosaur species was originally proposed for the North American forms (Long and Ballew, 1985). Osteoderms are very diversified morphologically, e.g., in proportions, variations in external ornamentation, and presence or lack of distinct spikes (e.g., Long and Murry, 1995; Parker, 2007, 2016). Long and Ballew (1985), introducing the first systematic of the North American aetosaurs, have based it solely on the most common paramedian osteoderms, arguing that the observed variability of the dermal armor is enough to establish the taxonomic divisions. They additionally supported this statement with an observation that differences in osteoderms within different systematic groups were congruent with the differences observed in the other parts of the skeleton, and expressed hope that the aetosaur armor could be a useful tool for biostratigraphic studies (Long and Ballew, 1985).

The idea of osteoderms being the most taxonomically informative parts of the skeleton became a paradigm of aetosaurian systematics. Its utility resulted in descriptions of numerous taxa from North America based entirely or almost entirely on osteoderms (e.g., Zeigler et al., 2002; Martz and Small, 2006; Spielmann et al., 2006; Lucas et al., 2007; Parker et al., 2008; Heckert et al., 2015; Parker, 2016). It also influenced cladistics analyses, dominated by dermal armor characters, following the assumption that osteoderms provide the main phylogenetic signal for the clade irrespective of the rest of the skeleton (e.g., Parker, 2007, 2008, 2016). However, as it seems to be true for most of the aetosaurs, there are several species with similarly shaped and ornamented osteoderms, that cannot be used for taxonomic identification, for example Aetosauroides scagliai, Aetosaurus ferratus, Calyptosuchus wellesi, Neoaetosauroides engaeus, Stagonolepis robertsoni, or Stenomyti huangae (e.g., Desojo et al., 2013). Nevertheless, it was demonstrated that despite having nearly identical osteoderms they differ significantly in other portions of skeleton, especially in the cranium (e.g., Desojo and Báez, 2005, 2007; Schoch, 2007; Desojo and Ezcurra, 2011; Small and Martz, 2013; Parker, 2016, 2018; Biacchi Brust et al., 2018).

Similar situations may occur within the genus *Paratypothorax* that was recorded from North America, Europe, Greenland, North Africa, and India (e.g., Kutty and Sengupta, 1989; Jenkins et al., 1994; Jalil et al., 1995; Long and Murry, 1995; Lucas et al., 2006; Schoch and Desojo, 2016), and until recently there was no other material known of this species except for osteoderms. It was originally introduced by Long and Ballew (1985) to distinguish osteoderms with similar proportions as Typothorax, but with radial ornamentation (not pitted as in the latter). In addition, unlike the other aetosaurs established by Long and Ballew (1985), Paratypothorax was based on both European and North American material (holotype SMNS 5721 comes from Germany), and until now it is not settled whether both represent a single species (e.g., Long and Ballew, 1985; Parker, 2016; Schoch and Desojo, 2016). Following the example of Aetosauroides scagliai, Calyptosuchus wellesi, Stagonolepis robertsoni and other aetosaurs with similar osteoderms, it seems unlikely that that globally distributed Paratypothorax represents a single taxon. In addition, the more recently described skull of an almost complete individual from Germany identified, based on the morphology of the osteoderms, as Paratypothorax and ressorum (SMNS 19003) is very similar to Aetosaurus ferratus. It was even suggested that they may be different growth stages of the same species (Schoch and Desojo, 2016). In regard to the above arguments, we consider the status of Paratypothorax uncertain and in need of further clarification.

# ARCHOSAUROMORPHA von Huene, 1946 ARCHOSAUROMORPHA indet. (Fig. 8D–E)

Material–ZPAL V.66/39 and ZPAL V.66/40, two small teeth. Description–Two isolated archosauromorph teeth were collected from Kocury. Both specimens are subcircular in crosssection, lacking the labyrinthodont structure, and with no visible serration. The isolated tooth ZPAL V.66/40 is preserved in two fragments (Fig. 8F). It has an indistinct striation on the crown. It is slightly compressed labiolingually.

ZPAL V.66/39 is a small (12 mm long) curved tooth (Fig. 8E). Longitudinal striations are preserved on both sides of the crown, a feature characteristic for some groups of archosauromorphs, (e.g., tanystropheids, dosweliids, phytosaurs, and dinosaurs; Ezcurra, 2016). Distinct carina lacking serration is visible on the specimen. Roemer (1870) referred an isolated tooth from Kocury to the phytosaur *Termatosaurus albertii*, known solely from the dental material. ZPAL V.66/39 resembles the specimen collected from Czarny Las illustrated by Roemer (1870), that was referred to the same species. Given the obscure material, *Termatosaurus albertii* is considered *nomen dubium* (Stocker and Butler, 2013). Additionally, the lack of dental synapomorphies of phytosaurs makes the attribution of the isolated teeth to that group difficult (Stocker and Butler, 2013).

#### ARCHOSAURIA Cope, 1869 ARCHOSAURIA indet. (Fig. 8A–C)

**Material**-ZPAL V.66/3, centrum of a vertebra; ZPAL V.66/7, skull bone (?nasal); ZPAL V.66/32, dorsal portion of the neural spine.

**Description**—ZPAL V.66/7 is a partially preserved bone with ornamented external surface, well-preserved suture, and visible edge of a fenestra (Fig. 8A, B). Development of those features suggests its archosaurian origin (see Nesbitt, 2011). Unfortunately, the specimen lacks characteristic elements that could allow unambiguous interpretation. We tentatively identify it as a nasal. Following this interpretation, the external ornamented

surface would be oriented dorsally, the suture would be for maxilla and would point ventrally, and the edge of the fenestra would delineate nares.

The dorsal surface is flat with traces of slight ornamentation, composed of longitudinal grooves, visible in the anterior and posterior part of the preserved portion. In lateral view the most posterior area of the preserved part, above the suture, abruptly rises, which may either indicate the presence of a tubercle or mark the elevation of the entire distal portion of the bone. The medial edge is thin and ends sharply with no trace of a suture. In dorsal view the lateral and medial edge form an acute angle between each other, which suggests an anterior taper. In anterior view the dorsal and lateral surfaces are set at an acute (close to right) angle. The anterior part of the preserved portion of a lateral wall creates a concave margin of the fenestra. The ventral edge of the lateral wall forms a thick sutural area. The suture is composed of numerous shallow grooves divided by thin laminae, positioned obliquely to the medial edge. A marked groove in the middle section of the sutural area seems to divide it in two parts: anterior with larger grooves and posterior with thinner grooves oriented at a more acute angle. Although the suture area clearly ends before it reaches the posterior edge of the lateral wall, it seems that the groove pattern continues posteriorly towards the end of the preserved area, but in less prominent form of tiny longitudinal scars. This area could be a suture with the lacrimal or an edge of another fenestra.

If interpreted as nasal, the overall shape of the bone is similar to that of aetosaurs in (1) having the dorsal surface ornamented and flat, but with an elevation above the suture with the maxilla (elevation is present for example in *Aetosauroides scagliai*, *Desmatosuchus smalli*, *Longosuchus meadei*, *Stagonolepis olenkae*); (2) being narrow mediolaterally, and anteriorly



FIGURE 8. Isolated archosauromorph and archosaur material from the Late Triassic of Kocury, Poland. **A,B**, ZPAL V.66/7, ?nasal bone in **A**, left lateral and, **B**, ventral views; **C**, ZPAL V. 66/32, dorsal portion of the neural spine in lateral view; **D**, ZPAL V.66/3, centrum of a vertebra in lateral view; **E,F** archosaur teeth: **E**, ZPAL V.66/39 and **F**, ZPAL V.66/40. Scale bar equals 1 cm.

narrowing; and (3) structure of the nares, as suggested by the short triangular maxillary process and possibly very long anterior process (Walker, 1961; Parrish, 1994; Small, 2002; Schoch, 2007; Sulej, 2010; Desojo et al., 2013; Schoch and Desojo, 2016; Biacchi Brust et al., 2018). However, there are two strong arguments against this reference. Firstly, in all known aetosaurs the ascending process of the maxilla inserts the socket in the nasal, so the nasal overlaps the maxilla (Walker, 1961; Parrish, 1994; Small, 2002; Desojo and Báez, 2007; Schoch, 2007; Small and Martz, 2013; Biacchi Brust et al., 2018), and this articulation seems to be developed in the same manner in the maxilla of Kocurypelta silvestris (ZPAL V.66/4). The morphology of the suture in ZPAL V.66/7 suggests that the maxilla would entirely overlap the nasal and there is no socket for the ascending process of the maxilla. On the other hand, the ascending process of the maxilla ZPAL V.66/4 is of comparable thickness as the maxillary process in ZPAL V.66/7, and at the tip of the ascending process, a similar pattern of grooves as in ZPAL V.66/7 is present. It is possible that the delicate lamina building the walls of the socket at the lateral side, which overlapped the maxilla, was broken and lost, but there is no trace of such a damage around the suture area in ZPALV.66/7. The second argument against the aetosaur origin of ZPAL V.66/7, if the specimen would be interpreted as the nasal, is that the medial edge of the bone, where the suture for another nasal should be, is very thin in comparison to the thick suture in other aetosaurs (Walker, 1961; Parrish, 1994; Small, 2002; Desojo and Báez, 2007; Schoch, 2007; Small and Martz, 2013; Biacchi Brust et al., 2018). If the bone is interpreted as the nasal and the area posterior to the suture of maxilla is interpreted as another fenestra, it could belong to a phytosaur, however, the fenestra would lack the elevation characteristic for this group (e.g., Chatterjee, 1978).

Alternatively, if all preserved edges would be interpreted as edges of fenestrae, the bone would have contact with three skull openings, which would place it in the posterior part of the skull. If the well-preserved edge of the fenestra, next to the sutural area, would be interpreted as the edge of the mandibular fenestra, then the bone could be a surangular of an archosaur (e.g., aetosaur), due to presumably elongated shape of the internal mandibular fenestra (Walker, 1961; Small, 2002; Schoch, 2007; Sulej, 2010; Small and Martz, 2013; Biacchi Brust et al., 2018), but it seems that the angle between the lingual and labial walls of the bone would be too obtuse.

ZPAL V.66/32 is a dorsal portion of the neural spine of a vertebra (Fig. 8C). The neural spine is narrow, and its dorsal portion expands laterally, forming a flat apical surface. This is a state typical for some archosaurs, including aetosaurs, phytosaurs, and rauisuchids (Nesbitt, 2011; Ezcurra, 2016).

ZPAL V.66/3 is a poorly preserved centrum of a probably anterior dorsal vertebra, given its length to height ratio and position of the parapophyses (Fig. 8D). The preserved portion suggests a relatively short centrum, being 86 mm high and 35 mm long, with only the posterior articular facet preserved, being spool-shaped and slightly concave. The anterior articular facet is eroded, revealing the hollowed-out interior of the centrum. On the left side, the proximalmost portion of the parapophysis is preserved. Dorsally, there is a relatively deep centrodiapophyseal fossa, which floor is punctured by at least two foramina. No keel is preserved on the ventral surface. Given the fragmentary nature of the specimen, its detailed taxonomic position is undetermined.

#### DISCUSSION

# Comparison of the Kocury Site with Other Localities from Poland

Our picture of the vertebrate assemblage from Kocury is far from being complete. We have been able to recognize so far only lungfish, turtle, aetosaur, neotheropod dinosaur, and indeterminate archosauromorph and archosaur remains. Among the localities with Upper Triassic sediments in Silesia, only Poreba displays a similar composition (Sulej et al., 2012; Niedźwiedzki et al., 2014). Lisowice, Woźniki, and Zawiercie-Marciszów vielded dicynodonts (Dzik et al., 2008; Budziszewska-Karwowska et al., 2010; Sulej et al., 2011a; Niedźwiedzki et al., 2011; Niedźwiedzki and Budziszewska-Karwowska, 2018; Sulej and Niedźwiedzki, 2019), synapsids mostly absent at that time in other parts of the world (Fröbisch, 2009). Despite the significant amount of material collected from Krasiejów and Poreba, that group has not been reported from those two sites so far. Aetosaurs and silesaurids are abundant among terrestrial vertebrates in Krasiejów (Dzik, 2003a; Dzik and Sulej, 2007; Fostowicz-Frelik and Sulej, 2010; Piechowski and Dzik, 2010; Sulej, 2010; Piechowski et al., 2014, 2019; Antczak, 2016; Dróżdż, 2018; Qvarnström et al., 2019a; Piechowski and Tałanda, 2020). Dinosauriform remains have been reported from Lisowice, Poreba, Woźniki, and Krasiejów (Sulej et al., 2011a, 2012; Niedźwiedzki et al., 2014; Kowalski et al., 2019; Qvarnström et al., 2019a). Kocury and Poreba differ from Lisowice in the presence of aetosaurs. The Poreba assemblage is dominated in abundance by proterochersid turtle remains (Sulej et al., 2012; Szczygielski and Sulej, 2016, 2019; Szczygielski, 2017; Szczygielski et al., 2018; Bajdek et al., 2019) that are unknown from the other localities in Poland except for the newly described material from Kocury.

The sites from Poland differ in their vertebrate composition from those of the south-western part of the Germanic Basin. Non-sauropod sauropodomorphs are common in Upper Triassic vertebrate localities such as Frick in Switzerland, Halberstadt and Trossingen in Germany, and Chassagne in France (e.g., Fraas, 1913a; Sander, 1992; Galton, 1998; Schoch and Seegis, 2014). Among thousands of bones recovered in the five Upper Triassic localities from Poland, no specimen can be unambiguously attributed to basal sauropodomorphs (see also discussion in Skawiński et al., 2017). However, the presence of these animals in the Norian-Rhaetian of Poland is supported by the ichnological record from the Skarszyny sequence in the Holy Cross Mountains (Gierliński, 2009; Niedźwiedzki, 2011). Another example differentiating the two areas of the Germanic Basin is the presence of a large carnivorous archosaur Smok wawelski Niedźwiedzki, Sulej and Dzik, 2012, in Lisowice and Zawiercie-Marciszów (Niedźwiedzki et al., 2012; Zatoń et al., 2015; Niedźwiedzki and Budziszewska-Karwowska, 2018; Qvarnström et al., 2019b), which is unknown from other parts of the world. Regarding turtles, two different lineages are known from the southern part of the basin, Proganochelyidae and Proterochersidae-but only the latter is known so far from the Polish localities (Szczygielski and Sulej, 2016).

Although the turtle Proterochersis porebensis is known from the adjacent Poreba locality, the unquestionable assignation of material from Kocury to that species is hampered by the fragmentary nature of the latter. The differences between the proterochersid species are minor in general and mainly apply to the number, shape, and size of the peripherals, the shape of the caudal notch, the connections of the eighth presacral vertebra, the characteristics of the carapacial scutes, and the overall size (Szczygielski and Sulej, 2016, 2019; Szczygielski et al., 2018). Nevertheless, Kocury is the second Triassic locality in southern Poland that has yielded remains of Proterochersis. It suggests that turtles were not as rare a component of the Late Trias ecosystems in that part of the Germanic Basin as was previously thought. Proterochersidae are also present in the Stubensandstein (Löwenstein Formation, Norian, a marginal equivalent of the Arnstadt Formation) in south-western Germany (Fraas, 1913b; Long and Ballew, 1985; Karl and Tichy, 2000; Lucas et al., 2006; Sulej et al., 2012; Joyce et al., 2013; Schoch and Desojo, 2016; Szczygielski and Sulej, 2016; Szczygielski, 2020).

To date, proterochersids are known exclusively from the Polish and German localities, although the fragmentary *Chinlechelys tenertesta* Joyce, Scheyer, Heckert and Hunt 2009, from the U.S.A. may also belong to this clade (Szczygielski and Sulej, 2019).

Lungfish tooth plates are common finds in the Triassic localities (Skrzycki et al., 2018). The lungfish tooth plate from Kocury (ZPAL V.66/5) differs from *Ptychoceratodus roemeri* from Krasiejów, *Ptychoceratodus silesiacus* from Lisów, and the lungfish from Lisowice and Poreba. It exhibits several features atypical for any *Ptychoceratodus* and *Ferganoceratodus* species. Surprisingly, the specimen exhibits similarities to the Cretaceous taxa like *Metaceratodus wichmanni* and *M. kaopen*. It may be a result of either a convergent evolution or an evolutionary relationship. Nevertheless, the specimen from Kocury increases the morphological, and potentially taxonomic diversity of the lungfish in the Germanic Basin.

Theropod remains are rare in the Triassic of Poland. The group was reported only in Lisowice, Poreba, and Kocury (Dzik et al., 2008; Niedźwiedzki et al., 2014; Skawiński et al., 2017). Among the silesaurid, herrerasaurid, and neotheropod materials collected from Poreba, only a proximal portion of the herrerasaurid fibula ZPAL V.39/46 can be compared with the holotype of *Velocipes guerichi* coming from Kocury. The bone differs from the holotype of *V. guerichi* in the absence of the medial groove and the presence of a notch on the anterior edge of the bone (Niedźwiedzki et al., 2014; Skawiński et al., 2017). The locality of Poreba also yielded remains of a neotheropod, but unfortunately the preserved material does not overlap with that collected from Kocury, hence comparison is impossible.

The aetosaurian osteoderms from Poręba were mentioned by Sulej et al. (2012) and referred to *Paratypothorax* sp. by Lucas (2015). They differ from the osteoderms referred here to *Kocurypelta silvestris* in (1) being more angular in shape; (2) having a different ornamentation pattern consisting of closely arranged radials and pits, which start sharply at the basis of the spike (in *K. silvestris* the ornamentation consists solely of radials, which are more widely distributed, and the transition between the ornamented and non-ornamented part is confluent); and (3) having a differently developed spike, which is more acute and expanded towards the cranial end of the osteoderm. Based on their morphology, the osteoderms from Poreba cannot be assigned to either the genera *Kocurypelta* or *Paratypothorax* (e.g., Long and Ballew, 1985; Lucas et al., 2006; Schoch and Desojo, 2016).

Two aetosaur species have been described from the Löwenstein Formation in Germany, namely Aetosaurus ferratus and Paratypothorax and ressorum (see Schoch, 2007; Desojo et al., 2013; Schoch and Desojo, 2016). They differ in the osteoderm morphology, as Pa. and ressorum presents dorsoventrally flattened spikes in the lateral osteoderms and significantly transversely elongated paramedian plates (Long and Ballew, 1985; Parker, 2007, 2016; Schoch, 2007). Phylogenetic analyses place A. ferratus in a basal position, and Pa. and ressorum as a derived member of Aetosauria (Parker, 2007, 2016; Desojo et al., 2013). The two aetosaurs from the western Germanic Basin have been considered globally distributed. However, this assumption was based on the occurrences of osteoderms (e.g., Lucas et al., 2006, Small and Martz, 2013, Parker 2016), given that little information about the rest of the skeleton was available. The only complete skeletons are known from Germany (A. ferratus from Kaltental, near Stuttgart, and Pa. and ressorum from Murrhardt; Long and Ballew, 1985; Jenkins et al., 1994; Lucas et al., 1998, 2006; Small, 1998; Schoch, 2007; Desojo et al., 2013; Schoch and Desojo, 2016). However, osteoderm morphology of A. ferratus is not diagnostic for the species. It was shown that at least some of the material from North America referred to A. ferratus in fact belong to a distinct taxon, namely Stenomyti huangae, as the Aetosaurus-like osteoderms were found with a skull of different morphology (Small and Martz, 2013). Similarly, Paratypothorax and Paratypothoracini are diagnosed based solely on the osteoderms (Long and Ballew, 1985; Lucas et al., 2006; Parker, 2007, 2016). So far, only a skull of the complete Pa. and ressorum specimen from Murrhardt has been described, and it shows a great similarity with the contemporary A. ferratus, suggesting that they may represent different growth stages of the same taxon (Schoch and Desojo, 2016). Nevertheless, it is uncertain whether the *Paratypothorax* material from Europe and North America represents the same taxon because they are recovered separately in phylogenetic analyses (e.g., Parker, 2016; Schoch and Desojo, 2016). Additionally, some osteoderm material from North America, referred to Paratypothorax, has been recently moved to a separate paratypothoracin genus, Tecovasuchus (see Martz and Small, 2006).

No Aetosaurus-like osteoderms have been collected so far from Poreba. The other Germanic Basin aetosaur from Krasiejów, Stagonolepis olenkae is very similar to the species from the Elgin sandstones in Scotland (Sulej, 2010; Antczak, 2016; Parker, 2016; Dróżdz, 2018). The aetosaur from Poreba was referred to paratypothoracin (Sulej et al., 2012) or Paratypothorax sp. (Lucas, 2015), presumably based on the presence of a dorsoventrally flattened spike. Yet it seems that the material from Poreba differs from Paratypothorax, and the new species from Kocury. Therefore, the aetosaurs of the Germanic Basin may be more diversified than previously thought. However, morphology of the osteoderms, although it possibly provides valuable phylogenetic and taxonomic information, is variable within the individual as well as intraspecifically, and little is known about changes in their ontogeny (Taborda et al., 2015; Parker, 2016; Schoch and Desojo, 2016). In addition, aetosaur material from the Polish localities beside Krasiejów is still scarce.

In summary, it seems that the composition of vertebrates from Kocury mostly resembles that of Poreba. Both assemblages yield remains of proterochersid turtles, neotheropod dinosaurs and typothoracin aetosaurs. This congruence may indicate that the vertebrate composition does not have an accidental (random) nature and that both localities represent remnants of similar ecosystems. However, despite the geographic proximity and taxonomic similarities, we could not establish temporal correlation between the two, due to the anatomical distinctions of the recognized animals and some differences in the lithology. Therefore, it is possible that, despite similar taphonomic conditions, they represent different times within the Late Triassic. The advanced features identified in aetosaurian, dinosaurian, and lungfish material might suggest a relatively younger age of the Kocury assemblage relative to localities in the Germanic Basin with comparable specimens. However, with the present data this remains a tentative hypothesis.

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