



Mammal-like tooth from the Upper Triassic of Poland

MARLENA ŚWIŁO, GRZEGORZ NIEDŹWIEDZKI, and TOMASZ SULEJ

Recent Triassic discoveries have extended the record of near-mammals (Mammaliaformes) back to the Norian, about 215 Ma, and reveal a significant diversity of Late Triassic (Norian-Rhaetian) forms. We now add to this Late Triassic diversity a nearly complete double-rooted right lower molariform tooth (ZPAL V.33/734) from the Polish Upper Triassic that is significant because it comes from uppermost Norian–lower Rhaetian rocks and is the first discovery of a mammal-like tooth in the Mesozoic of Poland. The described tooth shows transitional dental morphology between advanced cynodonts and mammaliaforms and it appears to represent a basal mammaliaform (genus *Hallautherium*), probably belonging to Morganucodonta.

Introduction

Mammal (sensu Kielan-Jaworowska et al. 2004) or mammaliaform (sensu Luo 2007) remains (mainly teeth) are known from numerous sites within Upper Triassic rocks, mainly in Western Europe, but also in Greenland and India. Collectively, these sites span the Norian through the end of the Rhaetian (see Clemens 1980, 1986; Datta and Das 1996; Kielan-Jaworowska et al. 2004; Datta 2005; Kemp 2005; Luo 2007). The latest Triassic mammaliaform faunas come from very different environments (e.g., lacustrine, deltaic, marginal-marine) and generally differ in composition and are usually dominated by, or solely contain, the remains of morganucodontids. Most of the Norian sites are dominated by remains of Haramiyida.

The most fossiliferous are Upper Triassic sites from continental Europe (Germany, France, Belgium, Switzerland, Luxembourg), but very important discoveries come from the Upper Triassic–Lower Jurassic fissure deposits of England and Wales, the lower part of the Tiki Formation in India, and Upper Triassic rocks of Jameson Land (Greenland) (see Kielan-Jaworowska et al. 2004; Datta 2005).

According to the fossil record from the Late Triassic and Early–Mid Jurassic, the diagnostic osteological features that have traditionally been associated with modern mammals did not evolve together at the same time (Luo 1994, 2007, 2011; Sidor and Hopson 1998; Kielan-Jaworowska et al. 2004; Rowe et al. 2011). A few features traditionally regarded as “mammalian” first appeared in the Late Triassic among their proximal relatives amidst the Mammaliaformes and Mammaliaforma, while other derived characters appeared for the first time only among Jurassic mammals. It is also clear that some mammalian

features have precursor conditions among derived cynodonts. Hence, the affinities of incomplete fossils are often difficult to assess. This applies especially to the teeth, which are very similar in morphology in basal mammaliaforms (e.g., *Brasilodon*, *Brasilitherium*) and mammaliaforms (e.g., *Sinoconodon*, *Morganucodon*, *Hadrocodium*), and which presumably also are similar in the ancestor of Mammalia (Luo et al. 2001; Bonaparte et al. 2005; Luo 2007). However, basal mammaliaforms teeth have less divided roots and undifferentiated postcanines.

Here we describe an isolated right lower molariform tooth of a probable early representative of mammaliaform, most likely morganucodontid (basal mammaliaforms), which comes from the Upper Triassic (Keuper) deposits of Poland. The specimen came from the lower part of the so-called grey unit, which is rich in plant and vertebrate remains and is exposed in a few places in the Lipie Śląskie clay-pit at Lisowice, Silesia, southern Poland (Fig. 1). The tooth was collected from this site in 2009 as part of a rock sample collected for the analysis of small fish fossils. Although isolated, this specimen deserves a short description in the literature, because it is consistent with morphology of mammaliaforms known from the Late Triassic and Early Jurassic elsewhere.

In the following description we adopt the terminology proposed by Crompton and Jenkins (1968) and used by other authors (e.g., Kielan-Jaworowska et al. 2004; Clemens 2011).

Institutional abbreviations.—PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological and stratigraphic setting

The strata exposed in the Lipie Śląskie clay-pit at Lisowice correspond to the uppermost part of the Middle and lower part of the Upper Keuper deposits of the Germanic Basin (Aigner and Bachman 1992; Szulc et al. 2006; Franz et al. 2007a, b; Franz 2008; Dzik et al. 2008a, b). The lithostratigraphic unit represented at the Lipie Śląskie clay-pit has traditionally been referred in the geological literature to the Norian (see Szulc et al. 2006) or to the Rhaetian “sensu polonico” (Haisig et al. 1983; Franz et al. 2007a, b; Franz 2008).

The vertebrate macrofossil assemblage from the Lipie Śląskie clay-pit consists mainly of terrestrial rather than am-

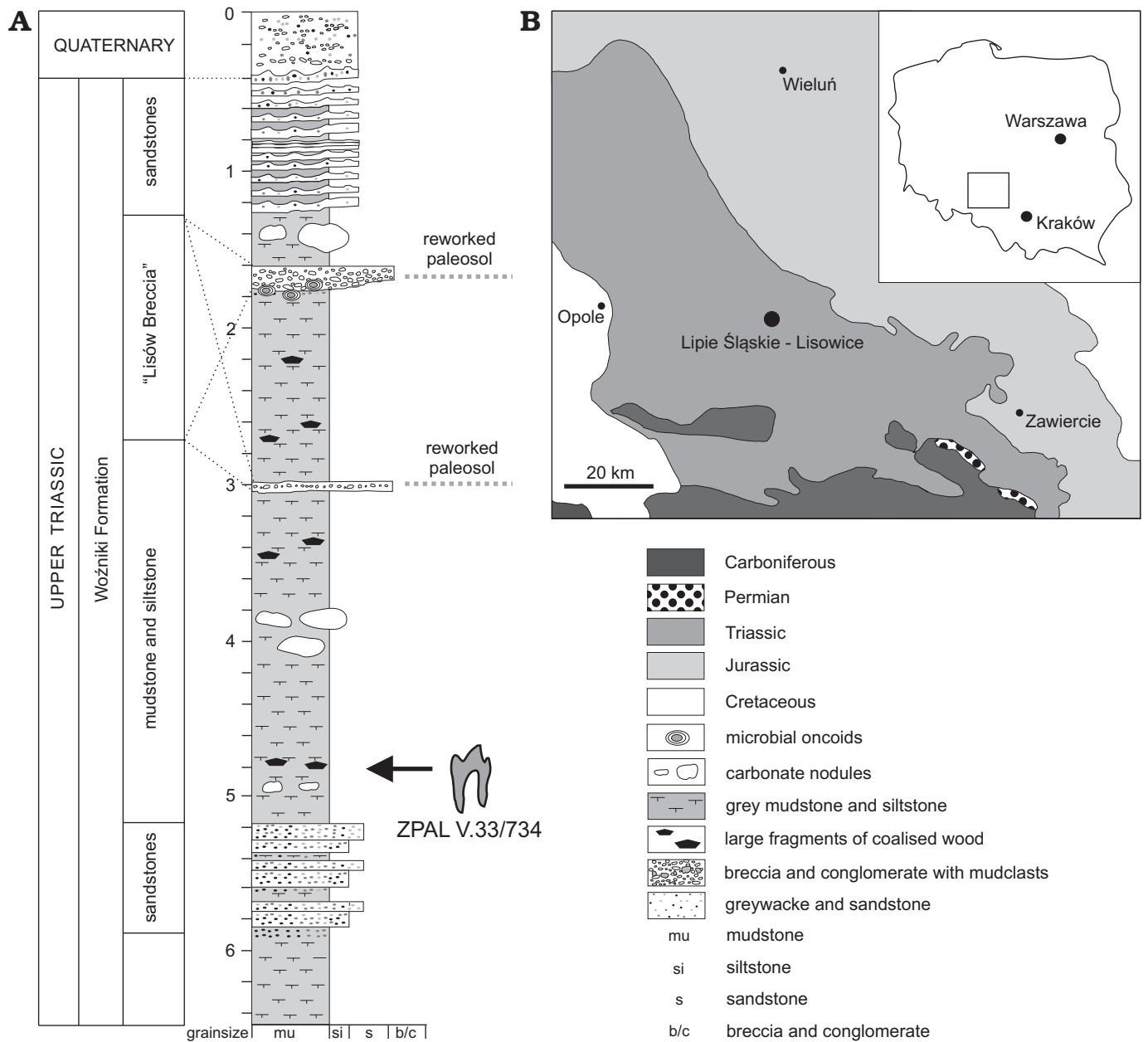


Fig. 1. A. Stratigraphic section of the Lipie Śląskie clay-pit at Lisowice. B. Location of the horizon that yielded ZPAL V.33/734, inset map showing position of locality in Poland.

phibious or aquatic tetrapods (Dzik et al. 2008a, b; Niedźwiedzki et al. 2011, 2012). Remains of a huge dicynodont are the most abundant finds and are followed by remains of the large predatory archosaur *Smok wawelski*, small to medium-size archosaurs (dinosauromorphs, dinosaurs, and poposaurids) and other archosauromorphs. Temnospondyls (*Cyclotosaurus* sp. and *Gerrothorax* sp.) are known from isolated, partially preserved skulls, skull bones, jaw bones, and numerous long bones. Like other bone-bearing sites of the Keuper unit in the Germanic Basin, the microfossils are dominated by remains of aquatic vertebrates and are comprised primarily of scales (or other dermal elements) and teeth of Actinopterygii, along with teeth, dermal denticles and fin spines of small sharks of the genera *Polyacrodus* and *Hybodus* (Świło 2010a–c; Świło and Kowalski 2011).

The only entirely aquatic macrofossils include numerous dental plates and skeletal elements of dipnoan fish (Dzik et al. 2008a). Other macrofossils represent mainly bones of land tetrapods.

Lithic characteristics and identification of palynomorphs: *Alisporites toralis* (Leschik) Clarke, 1965, *Todisporites cinctus* (Malliavkina) Orłowska-Zwolińska, 1971, *T. minor* Couper, 1958, *Anapiculatisporites spiniger* (Leschik) Reinhardt, 1962, *Anapiculatisporites telephorus* (Pautsch) Klaus, 1960, *Baculatisporites* sp., *Verrucosisporites* sp., *Foveolatitriletes crassus* Orłowska-Zwolińska, 1983, *Brachysaccus neomundanus* (Leschik) Mädlar, 1964, *Ovalipollis* sp. div., *Cedripites microreticulatus* Orłowska-Zwolińska, 1972, *Ricciisporites tuberculatus* Lundblad, 1954, *Rhaetipollis germanicus* Schulz, 1967, *Classopollis classoides* (Pflug) Pocock and Jansonius, 1961,

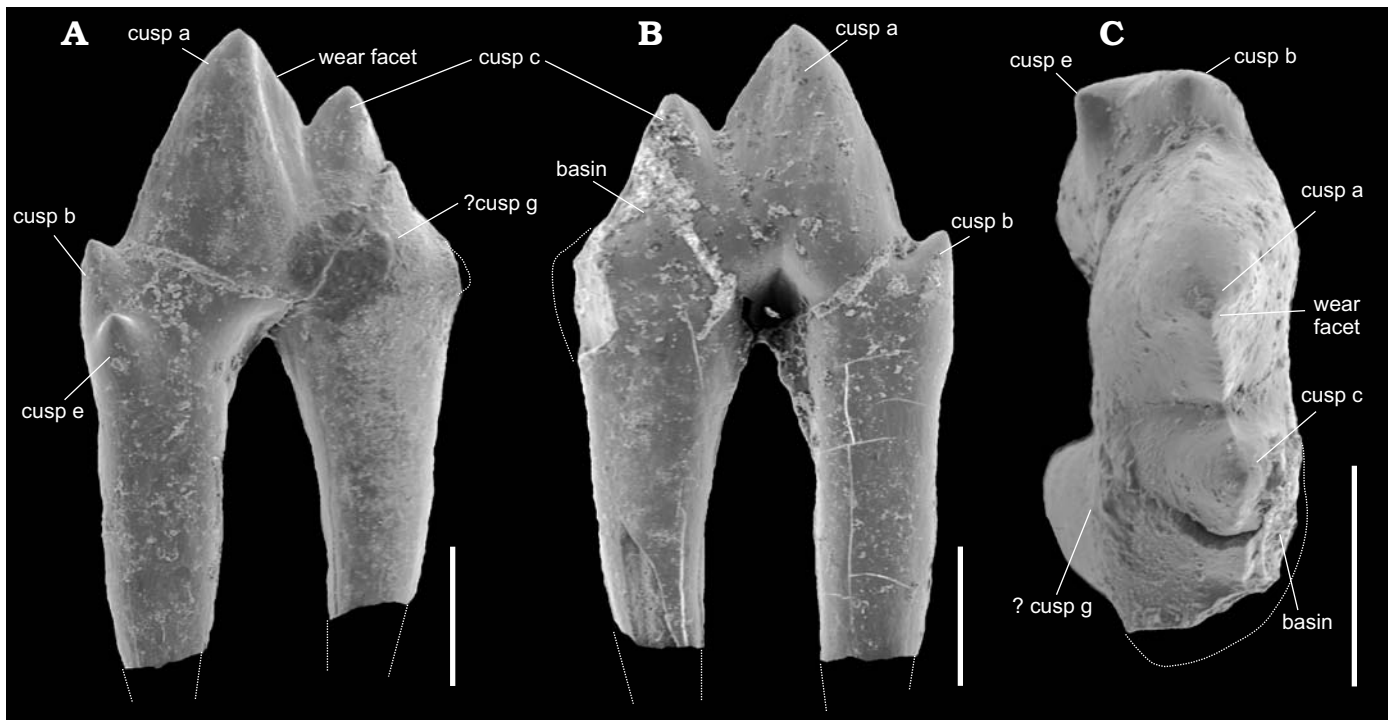


Fig. 2. SEM microphotographs of ZPAL V.33/734, right lower molariform tooth of the morganucodont mammaliaform *Hallautherium* sp. from Upper Triassic, Lipie Śląskie clay-pit at Lisowice, Poland; in lingual (A), labial (B), and occlusal (C) views. Scale bars 500 μ m.

Labiisporites triassicus Orłowska-Zwolińska, 1983, *Enzonalsporites* sp. div., *Triadispora polonica* Brugman, 1979, *Triadispora* sp., *Monosulcites minimus* Cookson, 1947, *Taurocusporites verrucatus* Schulz, 1967, *Porcellispora longdonensis* (Clark) Scheuring, 1970, cf. *Carnisporites megaspiniger* Morbey, 1975, *Eucommiidites* sp., *Nevesisporites limatulus* Playford, 1965, *Corollina meyeriana* (Klaus) Venkatachala and Góczán, 1964, *Granuloperculatiipollis rudis* Venkatachala and Góczán, 1964, in the grey and organic-rich strata at the Lipie Śląskie clay-pit suggest correlation of this unit with the uppermost Zbąszynek Beds and lower Wielichowo Beds (uppermost Norian–lower Rhaetian) from the northern part of Poland (Orłowska-Zwolińska 1983; Deczkowski 1997; Franz 2008). This lithostratigraphic unit apparently continues into the upper Löwenstein, Trossingen, and Exter formations of the Middle–Upper Keuper (upper Norian–Rhaetian) in the east German part of the Germanic Basin (see Franz et al. 2007a, b; Franz 2008), which contains the geologically oldest fossils of early mammaliaforms in the Germanic Basin (Clemens 1980; Kielan-Jaworowska et al. 2004; Seegis 2005).

According to lithologic descriptions of boreholes from central Poland (Dadlez and Kopik 1963; Deczkowski 1997) this unit is characteristic for the upper Zbąszynek and lower Wielichowo Beds from the north-western and central parts of Poland (Franz et al. 2007a, b; Franz 2008; Pieńkowski et al. 2012), and is also similar in part to a local informal lithostratigraphic unit named the Woźniki Formation from the Solarnia IG-1, Silesia (see Haisig et al. 1983). Such a simple lithostratigraphic correlation is also consistent with biostratigraphic (palynomorph data) correlation of the Lipie Śląskie exposure with boreholes from the Polish Lowland.

Suggestive of latest Norian–early Rhaetian age are finds of cuticle fragments of the typical Rhaetian seed-fern *Lepidopteris ottonis* (Goeppert, 1836) (Staneczko 2007); the conifer *Stachyotaxus septentrionalis* (this genus has a distribution strongly restricted to the Rhaetian of Scania and Greenland; see Taylor et al. 2009); the isoëtalean macrospores *Trileites* cf. *pinguis* (Harris, 1935) and *Horstisporites bertelseni* Fuglewicz, 1977 (Fuglewicz 1977; Fuglewicz and Śnieżek 1980); and the conchostracans *Gregoriusella polonica* Kozur, Niedzwiedzki, and Sulej, 2010, *Euestheria* sp., and *Shipingia* sp. (Kozur and Weems 2010). The species *G. polonica* is known from the lower Exter Formation of northern Germany (early Rhaetian) and the upper Redonda Formation of New Mexico, occurring above the *Shipingia olseni* Zone, correlated with the late Norian (Kozur and Weems 2010).

Systematic palaeontology

Mammaliaformes Rowe, 1988

Order Morganucodonta Kermack, Mussett, and Rigney, 1973

Family incertae sedis

Genus *Hallautherium* Clemens, 1980

Type species: Hallautherium schalchi Clemens, 1980; Hallau, Kanton Schaffhausen, Switzerland, Rhaetian.

Hallautherium sp.

Material.—ZPAL V.33/734 (lower molariform) from Upper Triassic, Lipie Śląskie clay-pit at Lisowice, Silesia, southern Poland.

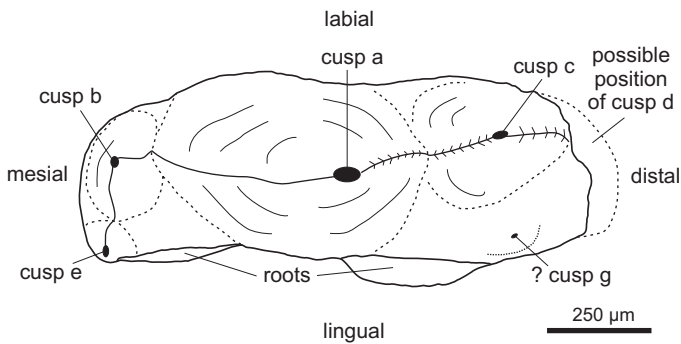


Fig. 3. Explanatory drawing of ZPAL V.33/734, right lower molariform tooth of the morganucodont mammaliaform *Hallautherium* sp. (occlusal view) from Upper Triassic, Lipie Śląskie clay-pit at Lisowice, Poland.

Description.—ZPAL V.33/734 is a very small, but nearly complete double-rooted right lower molariform with a main row of three (or even four, specimen is incomplete) cusps and additional anterior and posterior lingual cusps (Fig. 2). The mesio-distal length of the crown is 1.3 mm and the maximum width is 0.48 mm (Fig. 3). The height of the whole tooth, including roots is 3.19 mm. Tooth is in the size range of *Morganucodon watsoni*, *Hallautherium schalchi*, and *Morganucodon peyeri*. Its crown is clearly laterally compressed and primary cusps (a–c) are arranged longitudinally (Fig. 3). It is lower molariform, because the principal cusps a, b, and c are in line and the cusp a, the highest, is positioned slightly mesial to the middle of the crown. Additionally, cusp c is much larger than cusp b. Typically, in lower molariforms of Morganucodontidae, cusp g is large and situated lingual to the apex of cusp a, but in described specimen supposed cusp g is very small and situated lingual to the apex of cusp c.

The central cusp (cusp a), which is slightly flattened labio-lingually, is more massive than the mesial and distal ones and is slightly inclined distally. At the apex there is a small circular wear facet (Fig. 2). Crests run down from the apex, anteriorly toward cusp b and posteriorly toward the groove separating the main cusp from cusp c. The posteriorly-inclined crest is more pronounced. The distolingual part of cusp a is concave and shows wear (Fig. 2). In the specimen ZPAL V.33/734 the principal cusp (a) is anterior to the midpoint of the crown length.

Cusp b is conical and much smaller and lower than cusp a. It is located on the anterior part of the tooth. Mesio-lingual to cusp b is the slightly smaller cusp e, which is visible only on the lingual side. Cusp c is larger, and set much higher than cusps b and e. It is also closer to cusp a, separated from the cusp a by a shallow groove. It is cracked at the base in its distal part. Two crests run down from the top of cusp c. Just below cusp c, on the lingual surface, a small additional cusp is visible and most likely represents a poorly developed cusp g (Fig. 2). There is a small part chipped off at the distal edge of ZPAL V.33/734 (Fig. 3) where another small cusp (cusp d) may originally have been present. Neither surface (labial or lingual) of the lower part of the crown possesses a clearly marked cingulum, which supports identification of the specimen as a molariform of *Hallautherium*. As in *Hallautherium schalchi* but unlike any known morganucodontids a distal labial basin is present on ZPAL V.33/734

(in the form of a small depression on the described specimen). The roots are arranged mesio-distally and are massive at the base of the crown. They are very long and well separated, with a characteristic division up to the crown base (Fig. 3). Both roots are oval in outline. Pulp canals are open and the roots draw near each other at the ends.

ZPAL V.33/734 does not contain a cingulum, which is generally poorly developed in the molariforms of basal mammaliaforms, but is a characteristic feature of morganucodontid molariform teeth (e.g., Mills 1971; Kermack et al. 1973; Clemens 1980; Sigogneau-Russell 1983a, b; Hahn et al. 1991). ZPAL V.33/734 lacks a distinct system of wear facets and there is no evidence that this molariform was interlocked with an opposing tooth.

Discussion

In contrast to advanced non-mammalian cynodonts, and like in the molariforms of basal mammaliaforms (e.g., *Brasilitherium*) and early mammaliaforms such as *Hallautherium*, *Morganucodon* (e.g., Mills 1971; Kermack et al. 1973; Clemens 1980) or *Megazostrodon* (Crompton 1974; Gow 1986), ZPAL V.33/734 possesses cusps a–b–c–?–e (and also small cusp g). Presence of the cusp d is problematic because the fossil is broken. Additionally, ZPAL V.33/734 has roots that are more greatly separated from each other than in any known non-mammaliaform mammaliaform cynodonts, and also has a distinct root division up to the crown base, which is unique for teeth of Mammaliaformes.

The crowns of the lower molariforms of *Hallautherium schalchi* (specimens PIMUZ AIII-318 and AIII-337; see Clemens 1980) and in the lower molariform ZPAL V.33/734 are dominated by the relatively high principal cusp a, situated anterior to the midpoint of the crown. In addition, in *Hallautherium schalchi* and in the specimen ZPAL V.33/734 the two accessory cusps the posterior (c) is distinctly larger. All three teeth appear to have been supported by two, well separated roots.

The key similarity between *Hallautherium* and the specimen ZPAL V.33/734 is the well development of the disto-labial basin on the lower molariforms. In addition, presence of such a labial basin, which appears to have occluded with a cusp(s) of an upper molariform, is unknown in any species of *Morganucodon*, *Erythrotherium*, *Megazostrodon*, or *Eozostrodon* (Clemens 1980).

We consider ZPAL V.33/734 as an early mammaliaform molariform tooth (genus *Hallautherium*, order Morganucodonta; based on the following characters: 1, double-rooted tooth; 2, primary cusps a–c with additional cusp e and probably cusps d and g; 3, long and well separated roots with division close to the crown base; 4, presence of the disto-labial basin on the lower molariform; 5, cusp b is smaller than cusp c; and note that it has morphological features that distinguish it from teeth of all advanced non-mammalian cynodonts and basal mammaliaforms (e.g., tritheledontids, tritylodontids, probainognathids, brasilodontids, and dromatheriids). Double-rooted teeth and well separated roots do not occur in early mammaliaforms, which have incipient root division. However, *Brasilodon* and *Brasilitherium* have teeth that show root with a groove, which

could possibly be an early stage of a double-rooted tooth formation. The lower postcanines of brasilodontids bear a large central cusp flanked forward and backward by smaller, almost equal cusps b and c, which are arranged in mesio-distal line.

ZPAL V.33/734 shows a dental morphotype characteristic for representatives of morganucodontids and genus *Hallautherium* (Clemens 1980, 2011; Sigogneau-Russell 1983a, b; Hahn et al. 1991). This isolated tooth discovery probably represents a new taxon of Late Triassic (latest Norian–early Rhaetian in age) morganucodontid, but based on such an isolated tooth specimen it is not possible to describe a new species.

ZPAL V.33/734 is similar in age to the oldest fossils of morganucodontids in the Germanic Basin (they are latest Norian–Rhaetian in age) and is younger than the oldest fossils of dromatheriids, which are from the Turkey Branch Formation in Virginia (see Clemens 1980; Lucas et al. 2001), brasilodontids, which are late Carnian–early Norian in age (Bonaparte et al. 2005; Bonaparte 2013), and an isolated mammal-like tooth of an advanced cynodont (specimen SMNS 80766) from the Carnian of the Germanic Basin (Lucas et al. 2001). This find is significant as it is the first evidence of a mammaliaform taxon in the Upper Triassic deposits of the easternmost part of the Germanic Basin and it is also the second discovery of a mammalian fossil (and the first osteological specimen) in the Mesozoic of Poland (see Gierliński et al. 2004).

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Marlena Świło [marlena.swilo@pge.gov.pl], Institute of Palaeobiology, Polish Academy of Sciences, ul. Twarda 51/55, 00-818 Warszawa, Poland; Polish Geological Institute-National Research Institute, ul. Rakowiecka 4, 00-975 Warszawa, Poland;

Grzegorz Niedźwiedzki [grzegorz.niedzwiedzki@ebc.uu.se], Department of Organismal Biology, Uppsala University, Norbyvägen 18A, 752 36 Uppsala, Sweden;

Tomasz Sulej [sulej@twarda.pan.pl], Institute of Palaeobiology, Polish Academy of Sciences, ul. Twarda 51/55, 00-818 Warszawa, Poland.

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