

A new large capitosaurid temnospondyl amphibian from the Early Triassic of Poland

TOMASZ SULEJ and GRZEGORZ NIEDŹWIEDZKI



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The Early Triassic record of the large capitosaurid amphibian genus *Parotosuchus* is supplemented by new material from fluvial deposits of Wióry, southern Poland, corresponding in age to the Detfurth Formation (Spathian, Late Olenekian) of the Germanic Basin. The skull of the new capitosaurid shows an “intermediate” morphology between that of *Parotosuchus helgolandicus* from the Volpriehausen-Detfurth Formation (Smithian, Early Olenekian) of Germany and the slightly younger *Parotosuchus orenburgensis* from European Russia. These three species may represent an evolutionary lineage that underwent a progressive shifting of the jaw articulation anteriorly. The morphology of the Polish form is distinct enough from other species of *Parotosuchus* to warrant erection of a new species. The very large mandible of *Parotosuchus ptaszynskii* sp. nov. indicates that this was one of the largest tetrapod of the Early Triassic. Its prominent anatomical features include a triangular retroarticular process and an elongated base of the hamate process.

Key words: Temnospondyli, Capitosauridae, Buntsandstein, Spathian, Olenekian, Triassic, Holy Cross Mountains, Poland.

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Introduction

Tetrapod bones are rare in the Lower Triassic of Poland. An exception is the Czatkowice site in southern Poland, which has yielded one of the richest and most diverse tetrapod assemblage of the Germanic Buntsandstein Basin (Borsuk-Białynicka et al. 1999; Borsuk-Białynicka and Evans 2003; Paszkowski 2009). Among the Early Triassic (Olenekian) vertebrate fossils from the fissure infillings of the Czatkowice 1 locality, two taxa of temnospondyl amphibians have been recognized, the capitosaurid *Parotosuchus speleus* and the brachyopid *Batrachosuchoides* sp. (Shishkin and Sulej 2009). Both are represented almost entirely by remains of metamorphosed juveniles.

Isolated and poorly preserved vertebrate remains (mainly fragmented limb bones and ribs) have also been recognized from Buntsandstein strata on the northern margin of the Holy Cross Mountains (Senkowiczowa and Ślęczka 1962; Senkowiczowa 1970; Fuglewicz et al. 1981, 1990). Tetrapod remains, usually identified by geologists as “Labyrinthodontia indet.”, were collected at a few localities from the four

lithostratigraphical units in this region. Hitherto, only the finds from the Wióry locality were the subject of a short communication (Fuglewicz et al. 1981). Herein, we present a description of a new species of large parotosuchid temnospondyl, based on material collected at Wióry.

In Europe, the record of *Parotosuchus* includes two species from the Middle Buntsandstein of Germany, *P. nasutus* (Meyer, 1858) and *P. helgolandicus* (Schroeder, 1913), a single species (*P. speleus* Shishkin and Sulej, 2009) from the Czatkowice karst deposits of the Polish part of the Germanic basin, and a variety of species from European Russia designated as *P. bogdoanus* (Woodward, 1932), *P. orenburgensis* (Konzhukova, 1965), *P. orientalis* (Ochev, 1966), *P. panteleevi* (Ochev, 1966), *P. komiensis* (Novikov, 1986), along with *P. sequester* (Lozovsky and Shishkin, 1974) from Kazakhstan. Early Triassic rocks yield vast numbers of temnospondyl specimens in Gondwana, Russia, and a few spots in North America, but fail to do so in most places in Europe (Schoch 2011).

The objectives of this paper are to provide a description of the material of a new parotosuchid from the Late Olenekian of

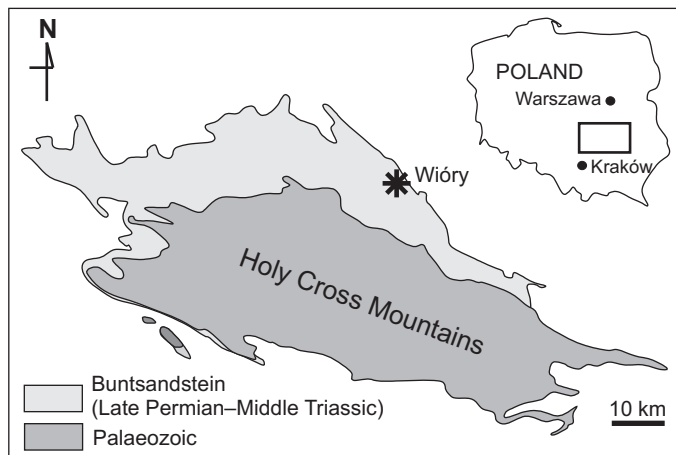


Fig. 1. Simplified geological map showing the Wióry locality in the northern margin of the Holy Cross Mountains, Poland.

Poland, and a discussion of parotosuchid capitosaurid evolution in Europe, based primarily on Olenekian specimens.

Institutional abbreviations.—MPT (MNtS), Museum of Nature and Technology (former Museum of History of Material Culture, MHkM) in Starachowice, Poland; PIN, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Geological background

The large outcrop at Wióry (Figs. 1, 2) resulted from the construction of a water barrage and reservoir on the Świślina River, from 1979 to 2005. The first vertebrate fossils from this site were discovered by Tadeusz Ptaszyński in autumn, 1980 (Niedźwiedzki and Ptaszyński 2007), and subsequently collected by Kazimierz Rdzanek, Mateusz Mielniczuk, Piotr Szrek, Paweł Król, and the authors (TS and GN). The largest collections (mainly tetrapod footprints) are deposited at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw and the Museum of Nature and Technology in Starachowice. Other collections also exist in other institutions (see Ptaszyński and Niedźwiedzki 2004). A number of specimens have also been gathered by amateur collectors.

The Wióry site is famous for its spectacular trace fossils (Fuglewicz et al. 1981, 1990; Ptaszyński 2000; Niedźwiedzki and Ptaszyński 2007; Brusatte et al. 2011), which include some of the earliest known fossils of the dinosaur stem-lineage. The ichnotaxa identified to date comprise 13 ichnospecies in 7 ichnogenera: *Capitosauroides* Haubold, 1971; *Brachychirotherium* Baurlen, 1959; *Isochirotherium* Haubold, 1971; *Synaptichnium* Nopcsa, 1923 (the last three ichnotaxa represent *Protochirotherium*–*Synaptichnium* plexus; see Klein et al. 2010); *Procolophonichnium* Nopcsa, 1923; *Rhynchosauroides* Maidwell, 1911; and *Prorotodactylus* Ptaszyński, 2000 (Fig. 2). Small and medium-sized Chirotheriidae tracks (made by Archosauromorpha; Haubold 1971a, b, 1984) and *Rhynchosauroides* tracks (ichnites

made by early Lepidosauromorpha or small Archosauromorpha; see Haubold 1971a, b; Avanzini and Renesto 2002) are dominant in this ichnoassemblage (Niedźwiedzki and Ptaszyński 2007; Brusatte et al. 2011). Unlike the footprints, body fossils are very fragmentary and rare at the Wióry site, rendering their identification difficult (until now about 100 fragmentary specimens have been collected). The bone material of the genus *Parotosuchus* collected from this locality is unique in its completeness.

The lithological sequence at Wióry comprises sandstone, mudstone, and claystone beds deposited in channels and floodplains of a braided river system (Mader and Rdzanek 1985; Fuglewicz et al. 1990). This sequence, informally named the Wióry Formation by Kuleta and Zbroja (2006), comprises the Labyrinthodontidae beds and the Hieroglyphic beds (sensu Senkowiczowa 1970; hieroglyphic—the name refers to the numerous horizontal invertebrate trace fossils discovered in those deposits), which have been correlated with the *Gervillia* beds (Goleniawy Formation sensu Kuleta and Zbroja 2006) of the lower part of the Middle Buntsandstein in the regional lithostratigraphic scheme (Kuleta and Zbroja 2006). The Wióry sequence yields numerous sedimentary structures (ripplemarks, desiccation cracks, rain drops), plant remains (horsetails and plant roots), two species of conchostracans (Ptaszyński and Niedźwiedzki 2006), and diverse invertebrate and vertebrate traces (Mader and Rdzanek 1985; Fuglewicz et al. 1990; Machalski and Machalska 1994; Rdzanek 1999; Ptaszyński 2000; Niedźwiedzki and Ptaszyński 2007).

The conchostracans *Magniesteria deverta* Novozhilov, 1946 (abundant on mudstone bedding surfaces), *Palaeolimnadia alsatica detfurthensis* Kozur and Seidel, 1983, and *Euestheria exsecta* Novozhilov, 1946 (both occasionally found on mudstone and siltstone intercalations) allows us to date the Wióry Formation as Late Olenekian and early Spathian (Bachmann and Kozur 2004; Kozur 2005; Kozur and Bachmann 2005; Ptaszyński and Niedźwiedzki 2006; Becker et al. 2007; Kozur and Weems 2010). This is consistent with the vertebrate ichnites from the Wióry Formation which are comparable with those of the Detfurth Sandstein, Detfurth Formation near Wolfhagen (Germany, North-Hessen) and those from the lower Hardegsen Formation (Hardegsen-Abfolge 1) near Gieselwerder (Fichter and Lepper 1997; Fichter and Kunz 2004), both Spathian in age (Bachmann and Kozur 2004; Kozur 2005; Kozur and Bachmann 2005).

The occurrence of the classical lower Anisian chirotherium ichnofauna (with *Chirotherium barthii*, *Ch. sickleri*) at a newly discovered site (Rzepin–Ostra Góra tracksite, about 10 km from Wióry), which is lithostratigraphically clearly located above the Wióry Formation, corroborates the Olenekian stratigraphical position of the Wióry site (Fig. 2).

Material and methods

Although the new material is very fragmentary, it shows characters that distinguish it from the other *Parotosuchus* species.

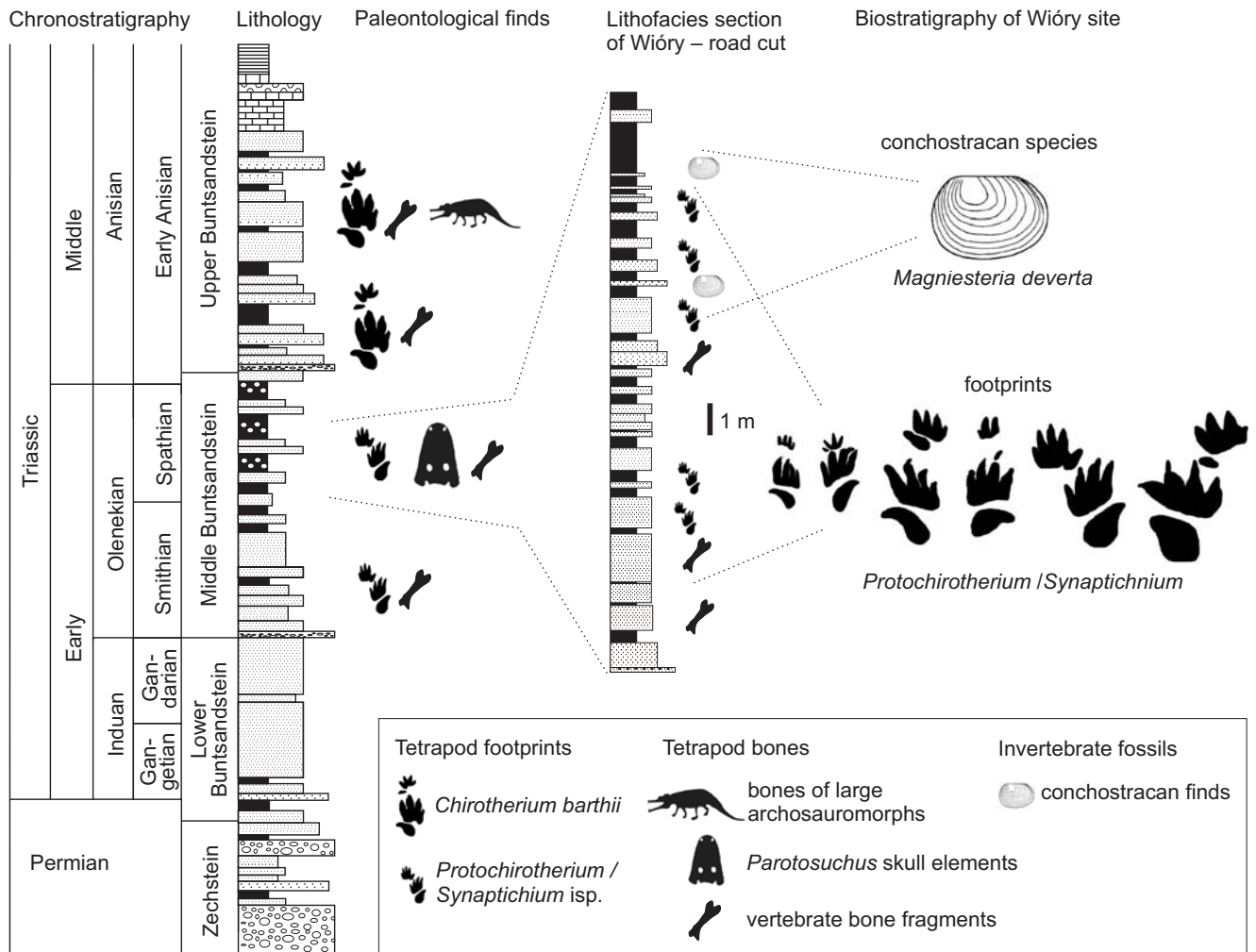


Fig. 2. Stratigraphic location of Wióry in the profile of the Buntsandstein from the northern margin of the Holy Cross Mountains (based on Ptaszyński and Niedźwiedzki 2006; Becker et al. 2007; Niedźwiedzki and Ptaszyński 2007).

The skull (MPT.P 271) is represented by the posterior part of the left side of the palate, which is preserved in a block of sandstone and exposed in dorsal view. Complete extraction of this skull fragment from the rock would be very difficult because the bone is extremely fragile. The preserved part of the skull consists of the bulk of the pterygoid, portions of the exoccipital, the ectopterygoid, the quadrate, the ventral processes of the tabular and postparietal, a fragment of the parasphenoid, and the ventral edge of the quadratojugal and jugal. The length of the skull was approximately 43 cm (along the midline). The position of some bones suggests that the skull is slightly compressed dorsoventrally, with its roof displaced towards the right. This is inferred from the position of the occipital condyle in relation to the tabular horn and from the strong rightwards inclination of the quadratojugal. The preserved part of the mandible (MPT.P 272) includes the middle and posterior portions of the left ramus, including the postglenoid region. Part of the lingual side of the postglenoid region and the hamate process are preserved as a thin remnant of the bone in the counterpart of the sandstone slab (Fig. 6). The length of the whole mandible was approximately 72 cm. A CT scan of

the skull was made to study the ventral part of the palate, but the poor state of preservation means the scan is useful in general morphological description, but is not of high quality.

Systematic palaeontology

Order Temnospondyli Zittel, 1890

Suborder Stereospondyli Fraas, 1889

Superfamily Capitosauroida Watson, 1919

Family Capitosauridae Watson, 1919
(= Mastodonsauroida Lydekker, 1885
sensu Damiani 2001a)

Genus *Parotosuchus* Ochev and Shishkin, 1968

Type species: *Parotosuchus nasutus* Meyer, 1858; Spathian of Germany.

Referred species.—*Parotosuchus helgolandicus* (Schroeder, 1913); *P. orenburgensis* (Konzhukova, 1965); *P. orientalis* (Ochev, 1966); *P. panteleevi* (Ochev, 1966); *P. sequester*

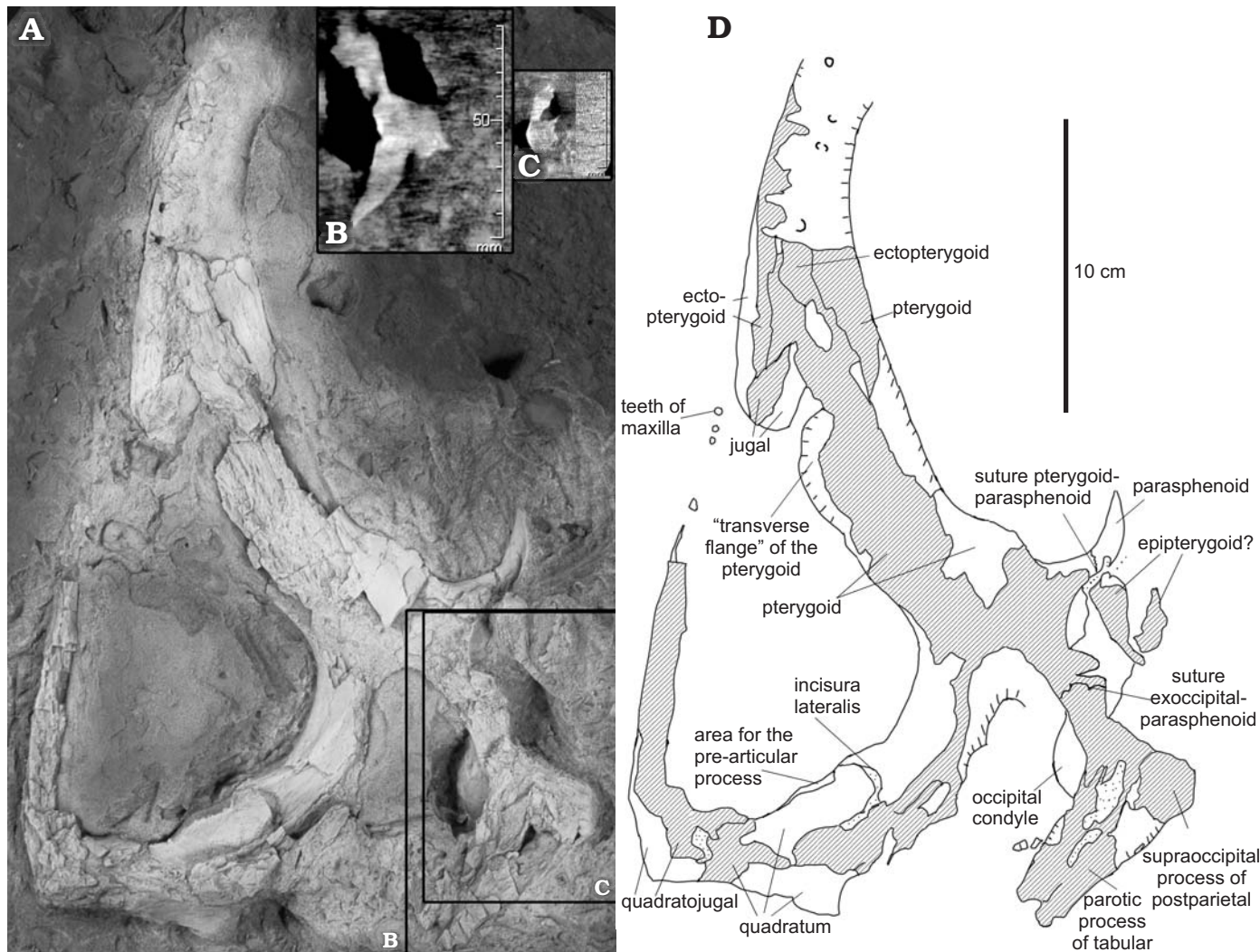


Fig. 3. Partial skull of capitosaurid amphibian *Parotosuchus ptaszynskii* sp. nov., Wióry, Late Olenekian, in a conglomeratic intercalation within a sandstone bed. **A.** Skull MPT.P 271 in dorsal view, coated with ammonium chloride. **B.** CT scan of the paroccipital process of the tabular and of the supraoccipital process of the postparietal. **C.** CT scan of the occipital condyle. **D.** Interpretative drawing.

Shishkin, 1974; *P. komiensis* Novikov, 1986; *P. speleus* Shishkin and Sulej, 2009, *Parotosuchus* sp. (in Welles 1947; see Morales 2005); *Parotosuchus* sp. (Sidor et al. 2007).

Remarks.—The species from the Middle Triassic of Gondwana described as belonging to *Parotosuchus* (Chernin and Cosgriff 1975; Mukherjee and Sengupta 1998; Damiani 2001a; see also Sidor et al. 2007) are considered to be generically distinct based on hyperelongated and exceptionally broad snouts, tabular horns that are postero-laterally directed and recurved, and other characters described by Damiani (2001b) in the diagnosis of *Cherninia*.

The assignment of the Wióry capitosaurid to *Parotosuchus* is based mainly on the structure of the mandible, which is preserved and well described only in *P. orenburgensis* among *Parotosuchus*. In both *P. orenburgensis* and the new species the retroarticular process is shorter than the glenoid area (new character) and its dorsal surface is sloped horizontally (character 47 in Maryńska and Shishkin 1996). The crista articularis is straight and horizontal in lin-

gual view. The Meckelian foramen has the length of a quarter or shorter of the adductor fossa length.

Geographic and stratigraphic range.—Late Early Triassic (Late Olenekian) of Europe, Africa, Antarctica, and North America.

Parotosuchus ptaszynskii sp. nov.

Figs. 3–7.

Etymology: In honour of Tadeusz Ptaszynski, paleontologist and geologist, who collected the mandible and many other bones and footprints at Wióry.

Holotype: Posterior part of a mandible MPT.P 272 (compressed, with the postglenoid area bent ventrally).

Type locality: Wióry, southern Poland (Holy Cross Mountains region).

Type horizon: Wióry Formation, Late Olenekian, early Spathian (see Ptaszynski and Niedźwiedzki 2006; Niedźwiedzki and Ptaszynski 2007; Becker et al. 2007).

Referred material.—Skull fragment showing the dorsal side of the posterolateral part of the palate MPT.P 271.

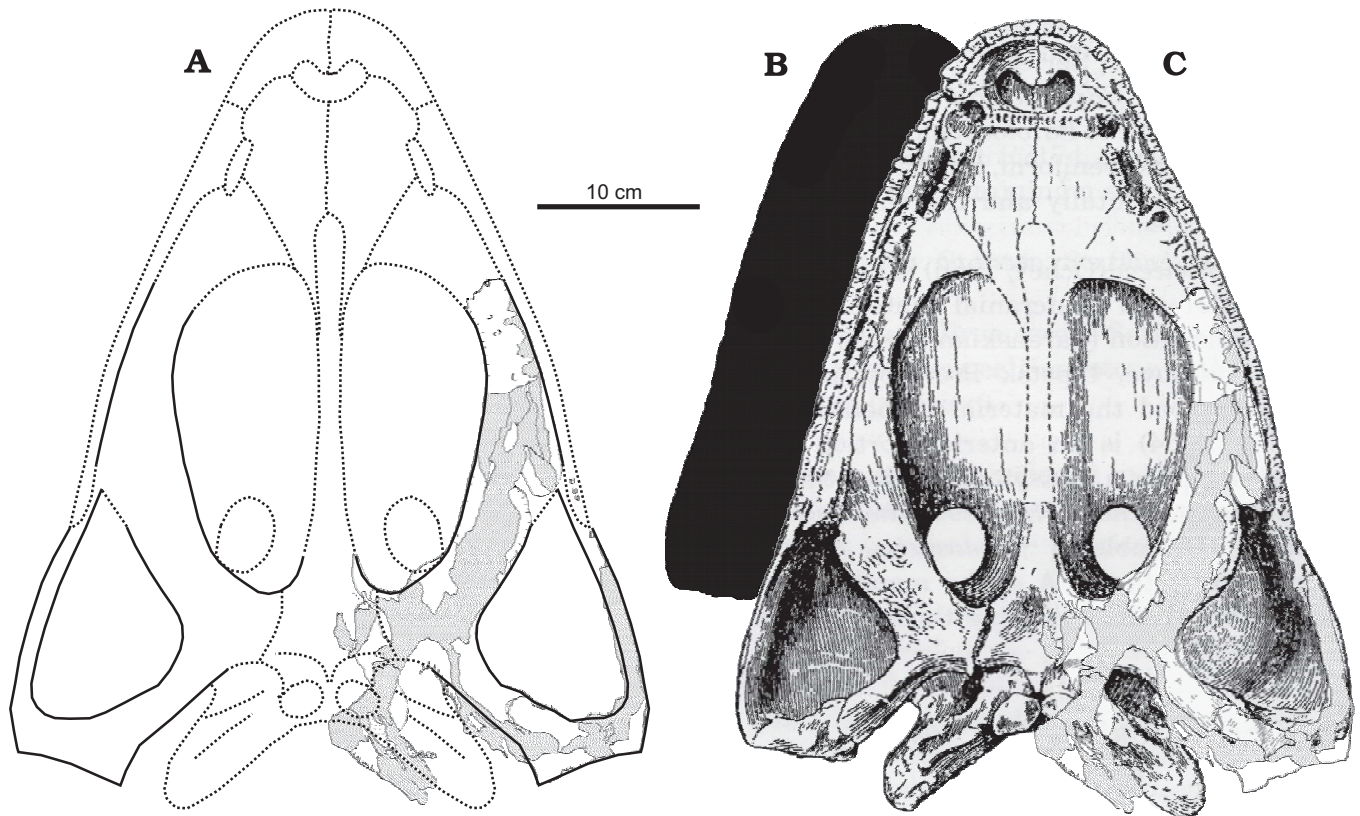


Fig. 4. Skull reconstruction (ventral view) of capitosaurid amphibian *Parotosuchus ptaszynskii* sp. nov., Wióry, Late Olenekian (A) and comparison with *Parotosuchus orenburgensis* (Konzhukova, 1965), Rossynaya, Ural River, Late Olenekian (C). The reconstruction of *P. ptaszynskii* sp. nov. based on the drawing of *P. orenburgensis* (from Konzhukova 1965); preserved fragment of *P. ptaszynskii* marked. B. Shadow of *P. orenburgensis* at the same scale as *P. ptaszynskii* in A.

Diagnosis.—*Parotosuchus* with the following combination of character states: torus arcuatus has more vertical position than the common condition in other parotosuchids. The dorsal surface of the retroarticular process is triangular, rather than roughly rectangular as in *P. haughtoni* and *P. orenburgensis*. The base of the hamate process is longer antero-posteriorly than in *P. haughtoni* and *P. orenburgensis*. The quadrate ramus of the pterygoid is shorter in length (= jaw articulation positioned more anteriorly) than in *P. helgolandicus*, *P. nasutus*, *P. haughtoni*, and longer than in *P. orenburgensis*. The lateral edge of the skull is more triangular in shape than in *P. orientalis* and *P. nasutus*.

Description

Skull

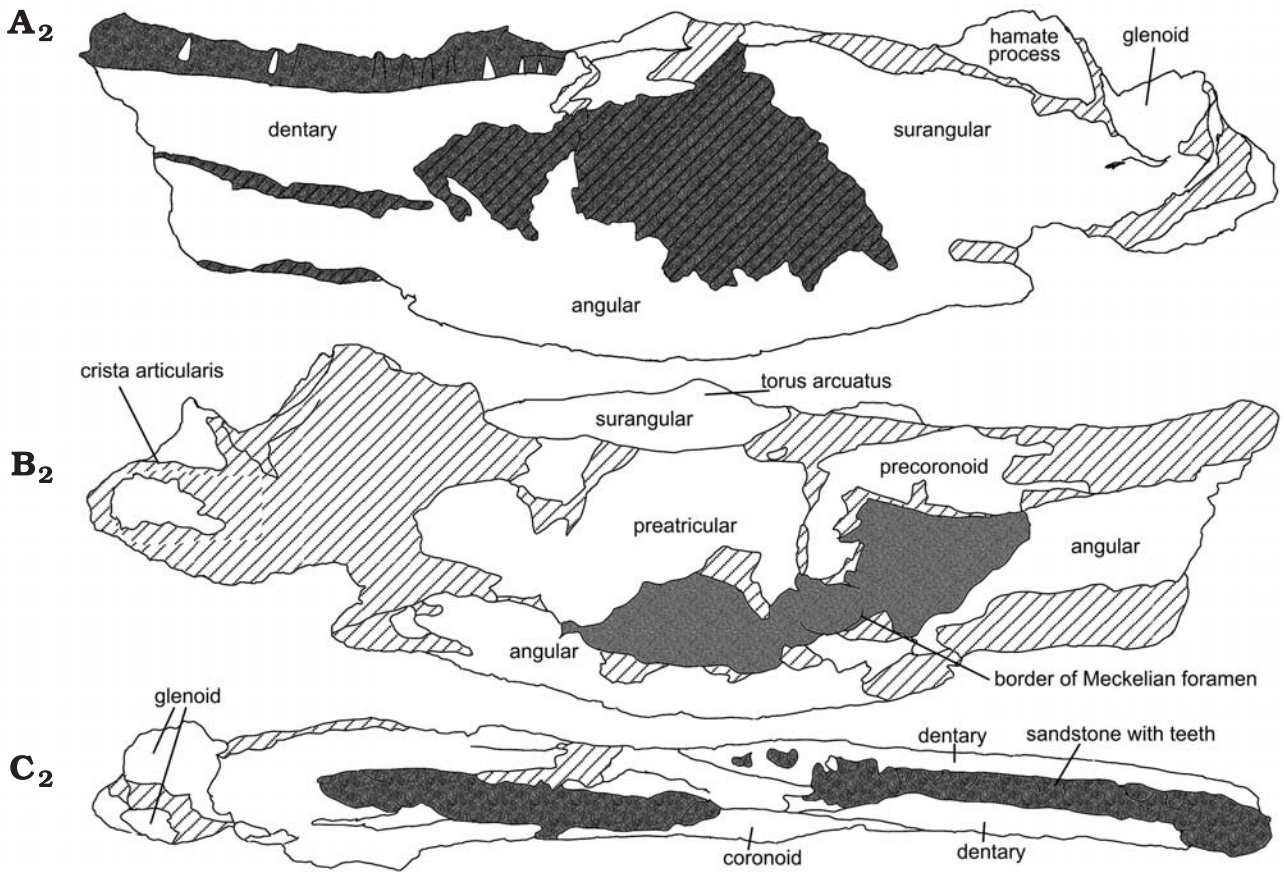
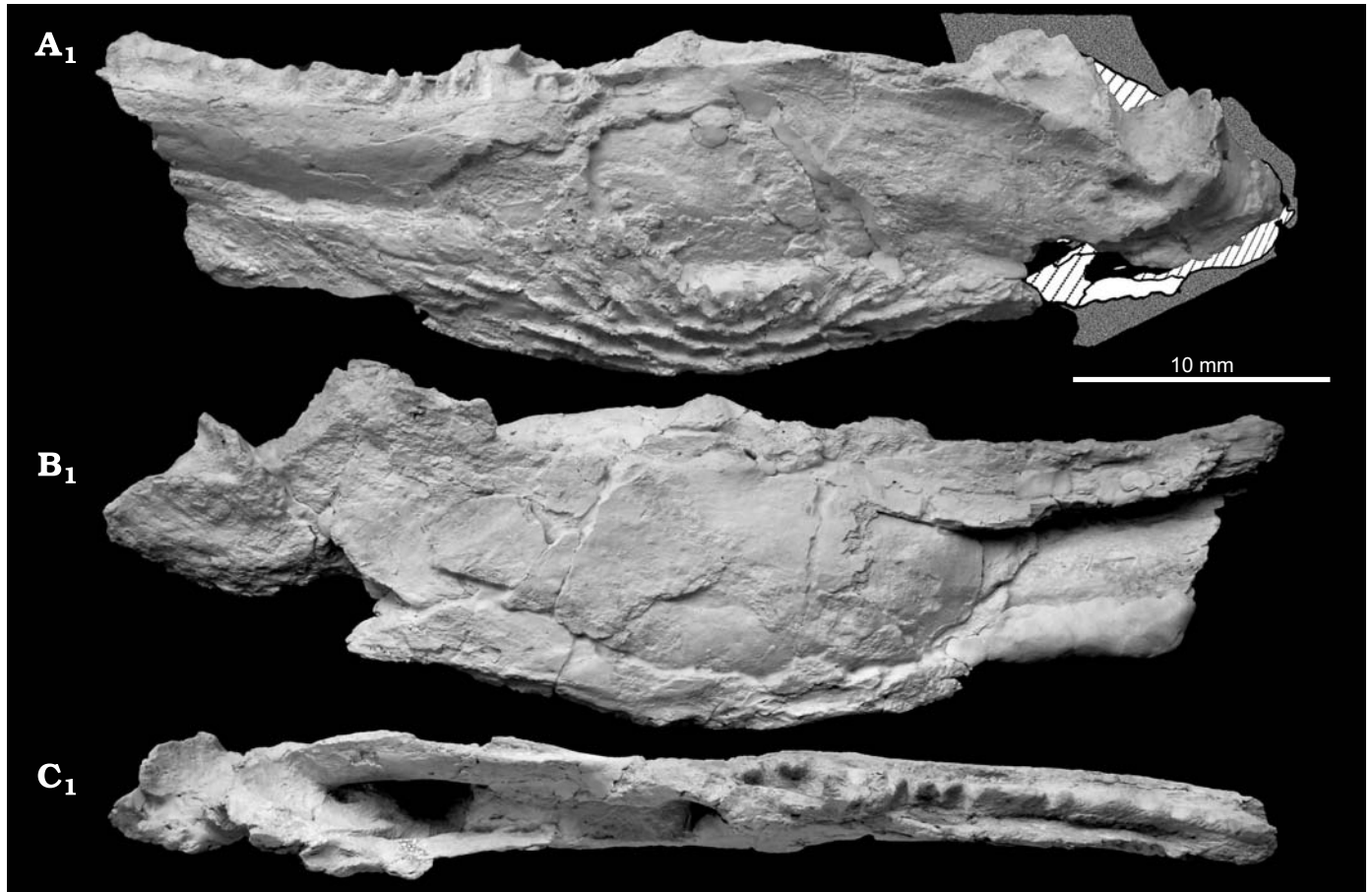
The general skull morphology is similar to that of *Parotosuchus orenburgensis*, especially the extremely strong curvature of the lateral edge of the interpterygoid fenestra. In all other *Parotosuchus* species this edge is much less concave, although the new material represents a larger skull than the holotype of *P. orenburgensis* (width of the skull PIN 951/42 is 315 mm while *P. ptaszynskii* is ~400 mm). The whole fenestra is wide and rather short (the shape of the palatine edge).

Ectoterygoid.—Although the small fragment of the left most

posterior part of this bone is preserved, the lateral edge of the element in this region is clearly visible. The fact that the lateral edge is very strongly curved is an evidence that the skull was narrowing anteriorly and was not elongated as in most parotosuchids (e.g., *Parotosuchus nasutus*, *P. helgolandicus*, *P. orientalis*).

Jugal.—The preserved part of processus alaris is massive and lay over the ectopterygoid.

Pterygoid.—The suture of the basiptyergoid ramus with the parasphenoid is clearly visible in its anterior part. It seems that this ramus is relatively wide and results in a very blunt posterior end of the interpterygoid foramen. On its dorsal side there is a distinct pocket with vertical edge, which is directed antero-posteriorly. This appears to be the ventral edge of the recessus conoideus (Bystrov and Efremov 1940). The quadrate ramus is rather long with its posterior end covered by the quadrate. The lateral edge of the quadrate ramus is directed strongly posteriorly making the medial edge of the temporal foramen strongly blunt. The palatine ramus is narrow and rather short, with a very distinct transverse flange. The medial edge of the palatine ramus is visible as an impression in the sandstone. At the base of this ramus a thin shelf protrudes anteriorly, disturbing the shape of the curvature of this margin (posterior edge of the interpterygoid foramen). The sutures with the ectopterygoid are partly visible.



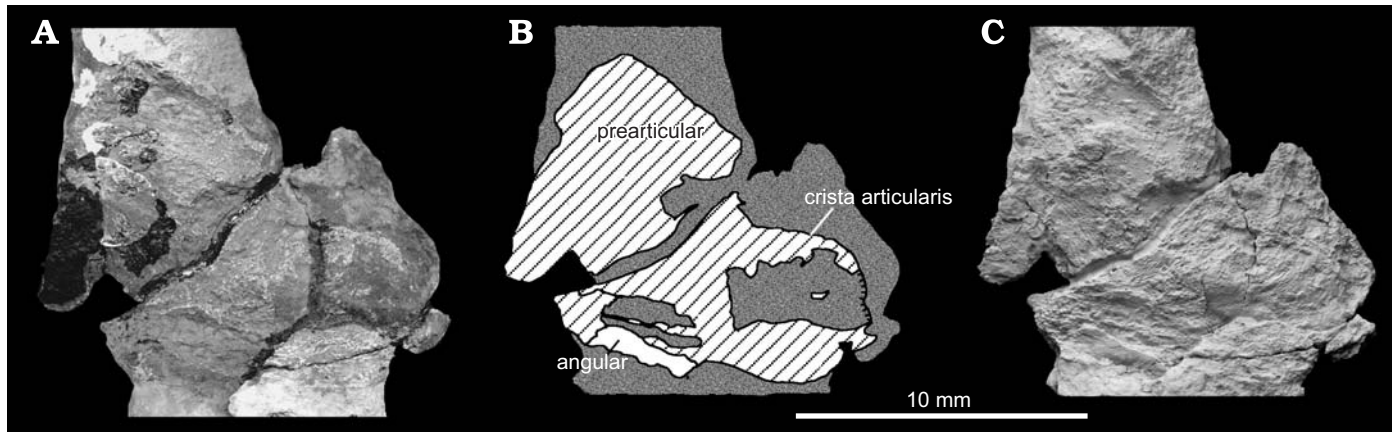


Fig. 6. Partially preserved mandible of capitosaurid amphibian *Parotosuchus ptaszynskii* sp. nov., Wióry, Late Olenekian, MPT.P 272, whitened. Sandstone with thin layer of bone tissue of the postglenoid region in lingual view (A), interpretative drawing (B), A whitened (C).

Palatine.—The medial edge of the palatine is visible as an impression in the sandstone. It is rather strongly concave in ventral view, very similar to *Parotosuchus orenburgensis* (Fig. 4).

Quadrate.—The anterodorsal part of the quadrate is preserved lying over the quadrate ramus of the pterygoid. Its medial end forms a distinct edge with a vertical wall. This morphology was first described for *Bentosuchus sushkini* by Bystrov and Efremov (1940) as the incisura lateralis, but it is better illustrated by Howie (1970). The same structure was observed in *Metoposaurus diagnosticus krasiejowensis* by Sulej (2007). Lateral to the incisura lateralis, on the anterior side of the quadrate, a sutural facet faces anterolaterally. According to Howie (1970) it articulates with the prearticular process of the mandible. Howie (1970) described it in *Stenocephalosaurus pronus* as present on the pterygoid but, in the new material described here, it occurs on the anterior edge of the quadrate.

Quadratojugal.—The ventral edge of the bone is straight. The anterodorsal process is directed medially and overlies the quadrate anterodorsally.

Exoccipital.—The suture of the exoccipital with the parasphenoid is visible only in cross section (of the crista paroccipitalis of the parasphenoid and the dorsal part of the exoccipital). The whole occipital condyle is here visible in the CT scan (Fig. 3B, C). Its articular surface is directed posteroventrally and is approximately 15 mm wide medio-laterally.

Mandible

The specimen belongs to a larger individual (about 72 cm skull length) than that represented by the above described skull fragment (skull approximately 43 cm long). The oval

Meckelian foramen is small and very short, and the torus arcuatus of the surangular has a very steep dorsal edge (Fig. 5). The base of the hamate process is longer in lateral view in *Parotosuchus ptaszynskii* than in the holotype of *P. orenburgensis*. As preserved, the postglenoid area of *P. ptaszynskii* appears to be more deformed than that of *P. orenburgensis*. The retroarticular process is shorter than the glenoid area and its dorsal surface is sloped horizontally (character 47 in Maryńska and Shishkin 1996). The crista articularis is straight and horizontal in lingual view (Fig. 6). The crista supraangularis which borders it labially is not so strongly convex in dorsal view as in *P. orenburgensis* (Maryńska and Shishkin 1996: fig. 22) and *P. haughtoni* (Damiani 2002: fig. 7 = *Kestrosaurus dreyeri* Shishkin et al. 2004: fig. 5), but this difference may result from the state of preservation of the Polish specimen. The chorda tympani foramen is not visible. The crista articularis is distinct as in *P. orenburgensis* (Maryńska and Shishkin 1996: fig. 22), but begins at the posterior part of the glenoid area as in *P. haughtoni* (= *Kestrosaurus dreyeri*; Damiani 2002: fig. 6). In *P. orenburgensis* it begins much more anteriorly (TS personal observation).

Discussion

The skull fragment and the mandible were found at the same locality, where large bone fragments are very rare. Their size differences indicate that they belonged to two different individuals. Without comparison to other better preserved fossils, showing that they represent the same species is impossible. The skull is identified as *Parotosuchus* based on its similarity to *Parotosuchus orenburgensis*. The holotype of *P. orenburgensis* (PIN 951/42) and the skull fragment from Wióry share the following characters: (i) a strongly concave lateral edge of the interpterygoid fenestra, (ii) skull that strongly narrows anteriorly, (iii) the parotic process of the tabular is directed at 45° to the long axis of the skull. This combination of characters is known only in these two species. The identification of the skull fragment is strengthened by the similarity of

← Fig. 5. Partially preserved mandible of capitosaurid amphibian *Parotosuchus ptaszynskii* sp. nov., Wióry, Late Olenekian, MPT.P 272, whitened. A. Lingual view, with contours of the postglenoid region, restored from the combination of the same specimen preserved as separate piece (see Fig. 6). B. Labial view. C. Dorsal view. Photographs (A₁–C₁), interpretative drawings (A₂–C₂).

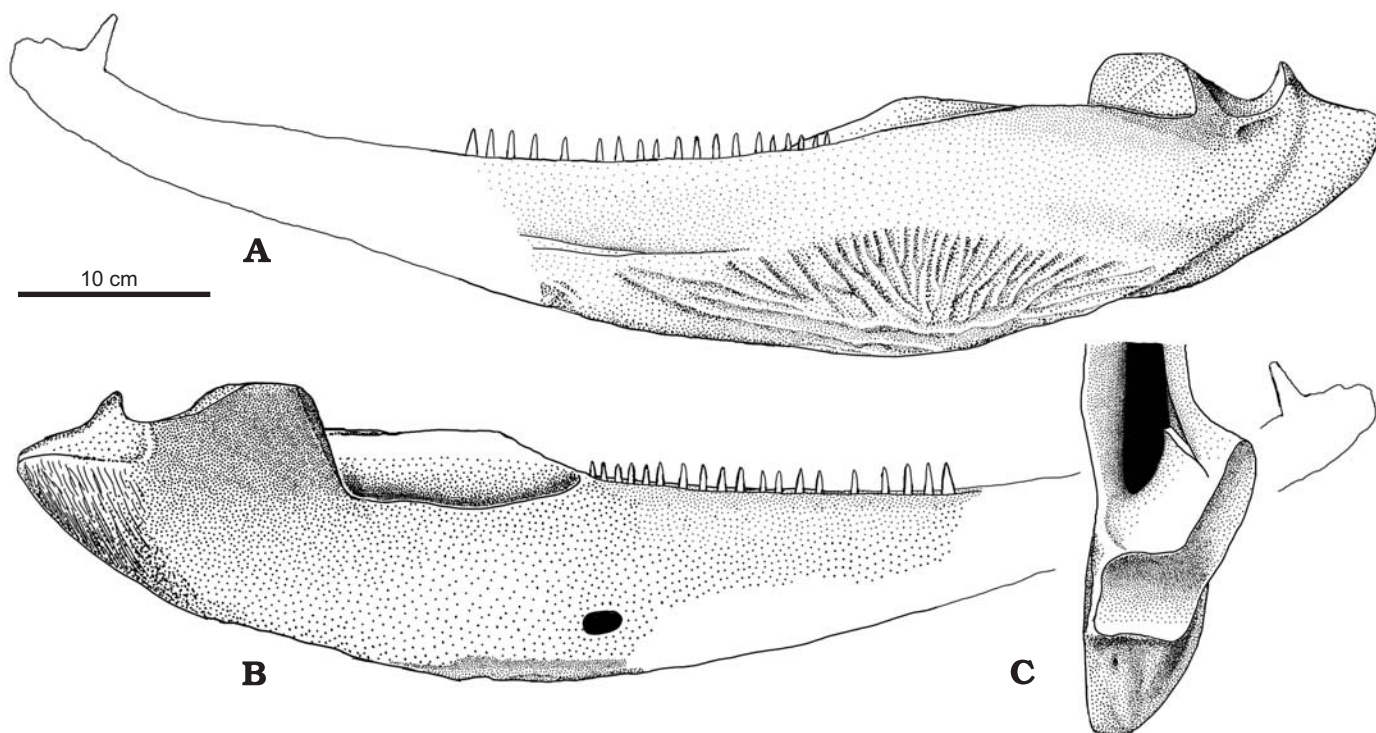


Fig. 7. Capitosaurid amphibian *Parotosuchus ptaszynskii* sp. nov., Wióry, Late Olenekian. Reconstruction of the mandible based on MPT.P 272. Anterior unpreserved part was based on the holotype of *Parotosuchus orenburgensis* (after Konzshukova 1965). Postglenoid region in labial (A), lingual (B), and dorsal (C) views.

the mandible fragment from Wióry to the holotype of the *Parotosuchus orenburgensis* (PIN 951/42). They share the following characters: (i) a very short Meckelian foramen, (ii) a strongly convex ventral edge of the mandible in lateral view, (iii) the retroarticular process is shorter than the glenoid area and its dorsal surface is sloped horizontally (character 47 in Maryńska and Shishkin 1996), (iv) the crista articularis is straight and horizontal in lingual view, (v) a very steep dorsal edge of the torus arcuatus of the surangular.

The capitosaurids appear in the Induan to Early Olenekian (Early Triassic), and include taxa such as *Wetlugasaurus*, *Rewanobatrachus*, *Edingerella*, and *Deltacephalus* (Schoch 2008). In Late Olenekian deposits, capitosaurids are represented by *Parotosuchus*, *Kestrosaurus*, *Cherninia*, *Odenwaldia*, *Stanocephalosaurus*, and the aberrant *Sclerotherax* (Shishkin et al. 1996; Damiani 1999, 2001a–c, 2002, 2008; Schoch 2000a, b; 2008; Schoch and Milner 2000; Damiani and Hancox 2003; Damiani and Rubidge 2003).

From the Olenekian, many species of large *Parotosuchus* species have been described from both northern and southern Pangea (Sidor et al. 2007). All of them display very elongate, slit-like choanae, and open otic notches (showing no clear trend to closure), and elongated, posterolaterally directed tabular horns. Some of these species are represented only by incomplete fossils, and therefore apomorphies are unknown. However most of them share the following characters: (i) retroarticular process of the mandible is shorter than glenoid area (Maryńska and Shishkin 1996, Damiani 2001a), with the dorsal margin of this process sloping horizontally (Maryńska and Shishkin 1996), and (ii) a crista articularis that is straight and horizontal in lingual view (new character).

During the Olenekian, two distinct *Parotosuchus* species are known from the Germanic basin, *P. helgolandicus* (Early–early Late Olenekian) and the younger *P. nasutus* (Late Olenekian) (Bachmann and Kozur 2005). Numerous species were also described from the Late Olenekian (Shishkin et al. 2000) of the European part of Russia and Kazakhstan. They are as follows: *P. orenburgensis* (Konzshukova, 1965), *P. pantelevi* (Otschev, 1966), *P. orientalis* (Otschev, 1966), *P. sequester* (Lozovsky and Shishkin, 1974), *P. ko-*

añska and Shishkin 1996), and (ii) a crista articularis that is straight and horizontal in lingual view (new character). Damiani (2001a) recognized two variable states of the length of the Meckelian foramen, long or short. According to him, the short Meckelian foramen is common among Triassic temnospondyls. Comparison of forms with this state of character described by Damiani (2001a) shows that only *Parotosuchus orenburgensis*, *P. haughtoni*, *P. ptaszynskii*, and *Rewanobatrachus aliciae* (sensu Damiani 2001a, different from all *Parotosuchus* in having an oval choana and V-shaped transvomerine tooth row), have the Meckelian foramen that is a quarter of the length of the adductor fossa or shorter. Other species analyzed by Damiani (2001a), including *Xenotosuchus africanus*, *Benthosuchus sushkini*, all *Eryosuchus* spp., *Lydekkerina*, and *Wellesaurus peabodyi* (sensu Damiani 2001a), have a Meckelian foramen that is approximately one third of the length of the adductor fossa or longer. Additionally, all forms which are represented by mandibular fossils (*P. orenburgensis*, *P. haughtoni*, and *P. ptaszynskii*) have a mandible with a strongly convex ventral margin in lateral view.

During the Olenekian, two distinct *Parotosuchus* species are known from the Germanic basin, *P. helgolandicus* (Early–early Late Olenekian) and the younger *P. nasutus* (Late Olenekian) (Bachmann and Kozur 2005). Numerous species were also described from the Late Olenekian (Shishkin et al. 2000) of the European part of Russia and Kazakhstan. They are as follows: *P. orenburgensis* (Konzshukova, 1965), *P. pantelevi* (Otschev, 1966), *P. orientalis* (Otschev, 1966), *P. sequester* (Lozovsky and Shishkin, 1974), *P. ko-*

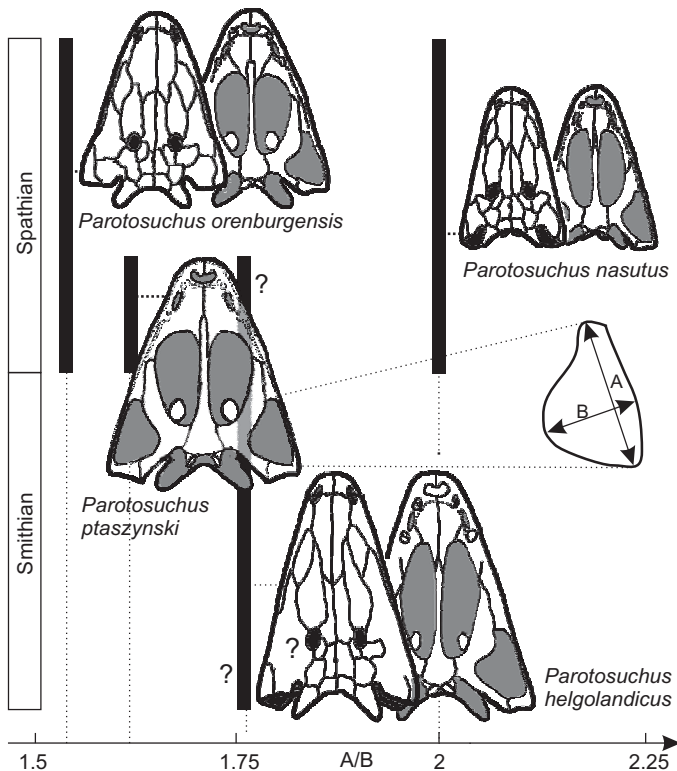


Fig. 8. *Parotosuchus* species from Europe (known from complete skull) in comparison with *Parotosuchus ptaszynskii* sp. nov. on stratigraphic plot with axis showing the proportions of the subtemporal fossa. *Parotosuchus helgolandicus* (Schroeder, 1913) and *Parotosuchus nasutus* (Meyer, 1858) (based on Welles and Cosgriff 1965), *Parotosuchus orenburgensis* (Konzhukova, 1965) (based on Konzhukova 1965).

miensis (Novikov, 1986), and *P. bogdoanus* (Woodward, 1932). Only the first is known from a complete skull and mandible. Recently, *P. speleus* was described on the basis of disarticulated skull bones of a juvenile (Shishkin and Sulej 2009). Furthermore, well preserved but still undescribed material of other *Parotosuchus* species has been reported from the Moenkopi Formation of North America (Schoch and Milner 2000; Lucas and Schoch 2002).

The form from the lower subzone of the *Cynognathus* Zone identified by Damiani (2002) as *P. haughtoni* (Broili and Schroder, 1937) is known from the most complete cranial material of any *Parotosuchus* species, which includes well-preserved palatal morphology.

Capitosaurid phylogeny has been discussed by many authors (Maryńska and Shishkin 1996; Schoch 2000a, b, 2008; Steyer 2003; Shishkin et al. 2004; Liu and Wang 2005; Stayton and Ruta 2006; Ruta et al. 2007; Schoch et al. 2007; Maganuco et al. 2009). Most of these authors utilized only one or two *Parotosuchus* species in their analyses, and then compared these exemplars with many other genera. In his cladistic analysis, Schoch (2008: 203) included *Rewanobatrachus rewanensis* (Warren, 1980) as *Watsonisuchus rewanensis*, as well as *Parotosuchus haughtoni* (sensu Damiani 2001a), *P. orenburgensis*, and *P. nasutus*. According to his results, *Watsonisuchus rewanensis* is the sister taxon

of a clade comprising *Parotosuchus* and the other capitosauroids (node 8 of Schoch 2008: fig. 8).

Parotosuchus helgolandicus (Schroeder, 1913) from the lower part of the Middle Buntsandstein, Volpriehausen Formation or Detfurth Formation, Smithian–lower Spathian, Germany (after Bachman and Kozur 2005), seems to be one of the closest in age to the new Polish species. Although in the original description of this German taxon Schroeder (1913) did not mention the exact locality and horizon of discovery, this species is from Helgoland Island where only sediments of the Volpriehausen and Detfurth Formations occur (Bachman and Kozur 2005). It differs from *P. ptaszynskii* in the following characters: (i) the skull is elongated (although it is narrower—skull width is 364 mm, contrary to ~400 mm for *P. ptaszynskii*); (ii) the interpterygoid and subtemporal fenestrae are elongated.

Younger than *P. helgolandicus* is *P. nasutus*, also from Germany. It originates from the lower Solling Formation (Rainer Schoch, personal communication 2009) (Spathian). It is similar to the previous form in that the interpterygoid and subtemporal fenestrae are elongated and the quadrate ramus of the pterygoid is long. All these characters distinguish it from *P. ptaszynskii*.

In the Cis-Urals of Russia, *Parotosuchus orientalis* Ochev, 1966 is known from the lower part of the Petropavlovskaya Formation, belonging to the Yarenskian Stage, Spathian, and *Parotosuchus orenburgensis* Konzhukova, 1965 from the same formation (Shishkin et al. 2000). Both species are closest in age to the new taxon. The subtemporal fossa in *P. ptaszynskii* is almost identical in proportions to that in *P. orientalis* (skull width is ~380 mm). The shape of the interpterygoid fenestra is unknown but the position of the maxilla shows that the whole skull was rather elongated as in *P. helgolandicus* and *P. nasutus*.

Information from the age and skull morphology of the European *Parotosuchus* species known from the skull suggests some aspects of the evolution of this genus. The ratio of length to width of the temporal fenestra is: *P. helgolandicus*, 1.76; *P. ptaszynskii*, 1.62; *P. orenburgensis*, 1.54 (Fig. 8). It seems that *P. ptaszynskii* is intermediate in age and morphology between *P. helgolandicus* and *P. orenburgensis*. The relationships of *P. nasutus* are unknown.

Conclusions

The new material of *Parotosuchus* from the early Spathian of Poland represents a new species morphologically intermediate between congeneric finds in Germany and Russia. This suggests a lineage persisting in Europe through the Late Olenekian, with changes occurring mainly in the shape of the skull and interpterygoid and subtemporal fenestrae.

At the end of the Early Triassic (Late Olenekian), important environmental changes took place in the marginal parts of the Germanic Basin. Rivers became larger and developed from small local gullies over braided river systems into fast-

changing, larger meandering rivers covering larger areas (Mader 1981; Mader and Rdzanek 1985; Fuglewicz et al. 1990). Such large rivers and small lakes from alluvial plains created niches for large aquatic temnospondyls. Large-bodied predatory temnospondyls (*Parotosuchus*, *Trematosaurus*, *Sclerothorax*, *Odenwaldia*, *Meyerosuchus*) are widely known from the Upper Olenekian deposits of the Germanic Basin (Schoch 2011). It is possible that these environmental changes may have stimulated the origin and early evolution of the large capitosaurids.

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