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To cite this article: Hans-Dieter Sues , Rainer R. Schoch , Gabriela Sobral & Randall B. Irmis (2020) A new archosauriform reptile with distinctive teeth from the Middle Triassic (Ladinian) of Germany, Journal of Vertebrate Paleontology, 40:1, e1764968, DOI: [10.1080/02724634.2020.1764968](https://doi.org/10.1080/02724634.2020.1764968)

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ARTICLE

A NEW ARCHOSAURIFORM REPTILE WITH DISTINCTIVE TEETH FROM THE MIDDLE TRIASSIC (LADINIAN) OF GERMANY

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ABSTRACT—Skeletal remains of a small reptile with a distinctive dentition from the Lower Keuper (Erfurt Formation; Middle Triassic, Ladinian) of the Schumann quarry near Eschenau, in the municipality of Vellberg in Baden-Württemberg, Germany, represent a new taxon of non-archosaurian archosauriforms, *Polymorphodon adorfi*. It is diagnosed by various craniodental autapomorphies, including mesial and distal carinae of labiolingually flattened maxillary and dentary tooth crowns with large, somewhat hook-shaped denticles aligned at distinct angle to apicobasal axis of tooth crown; premaxilla with long, leaf-shaped posterodorsal process that is slightly longer than body of element; presence of prominent lateral fossa on premaxilla anteroventral to external narial fenestra; premaxilla with five gently recurved, conical teeth; medial surface of maxilla with distinct ledge above the interdental plates; and maxilla and dentary with distinctly heterodont dentition. Phylogenetic analysis recovered *Polymorphodon adorfi* in a position crownward of *Erythrosuchus africanus* but in an unresolved polytomy with derived non-archosaurian archosauriforms such as Proterochampsidae and *Euparkeria capensis* and with Archosauria. The maxillary and dentary teeth of *Polymorphodon adorfi* differ from those of other non-archosaurian archosauriforms and indicate a different, possibly omnivorous diet, suggesting that these reptiles were more diverse in terms of feeding habits than previously assumed.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Sues, H.-D., R. R. Schoch, G. Sobral, and R. B. Irmis. 2020. A new archosauriform reptile with distinctive teeth from the Middle Triassic (Ladinian) of Germany. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2020.1764968.

INTRODUCTION

Archosauria is a particularly diverse clade of amniotes and includes some of the most spectacular reptiles that ever existed. Only two clades, crocodylians and birds, have survived to the present day. For many years, archosaurs were divided into dinosaurs (including birds), pterosaurs, and crocodylians, along with a number of mostly Triassic-age taxa variously related to these groups. Boulenger (1903) and Watson (1917) united the latter taxa in a group for which they used Owen's (1859) name Thecodontia. Over the years, this definition became generally adopted and Thecodontia came to be viewed as the ancestral stock from which all other archosaurs arose (e.g., Romer, 1956, 1972). Gauthier (1986) first distinguished two major lineages among Archosauria, one leading to crocodylians (Pseudosuchia) and the other to dinosaurs and their descendants, birds (now named Avemetatarsalia). Many 'thecodontians' have subsequently been assigned to one of these two lineages. Although closely related to Archosauria, some 'thecodontians' are more basal than the most recent

common ancestor of crocodylians and birds and thus are not crown-group archosaurs. Gauthier et al. (1988) grouped these taxa with archosaurs in the clade Archosauriformes. In recent decades, new discoveries have documented an unexpected diversity of body plans among non-archosaurian archosauriforms (Foth et al., 2016; Li et al., 2016; Stocker et al., 2016). Here, we report on a new taxon of non-archosaurian archosauriform from the Middle Triassic (Ladinian) of Baden-Württemberg, Germany. It provides additional evidence that non-archosaurian archosauriforms were more diverse in terms of body plans and feeding habits than previously assumed.

The new taxon is based on two partial skeletons that were collected from mudstones of the Middle Triassic (Ladinian) Erfurt Formation (Lower Keuper or Lettenkeuper) exposed in the Schumann limestone quarry southeast of Eschenau, in the municipality of Vellberg in Baden-Württemberg, Germany, during the summer of 2010. This locality has yielded a wealth of skeletal remains documenting a diverse assemblage of late Middle Triassic vertebrates (Hellrung, 2003; Schoch, 2006, 2008; Witzmann et al., 2008; Damiani et al., 2009; Jones et al., 2013; Sues and Schoch, 2013; Schoch and Sues, 2014, 2015, 2018a, 2018b; Schoch et al., 2018; Witzmann and Schoch, 2018). The fossiliferous layer of gray mudstones attains a thickness between 5 and 15 cm (unit E6 of Schoch and Seegis, 2016; Fig. 1) and was probably deposited in a relatively small lake (Schoch and Seegis, 2016). It has yielded remains of the

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This article was originally published with errors, which have now been corrected in the online version. Please see Correction (<http://dx.doi.org/10.1080/02724634.2020.1791513>)

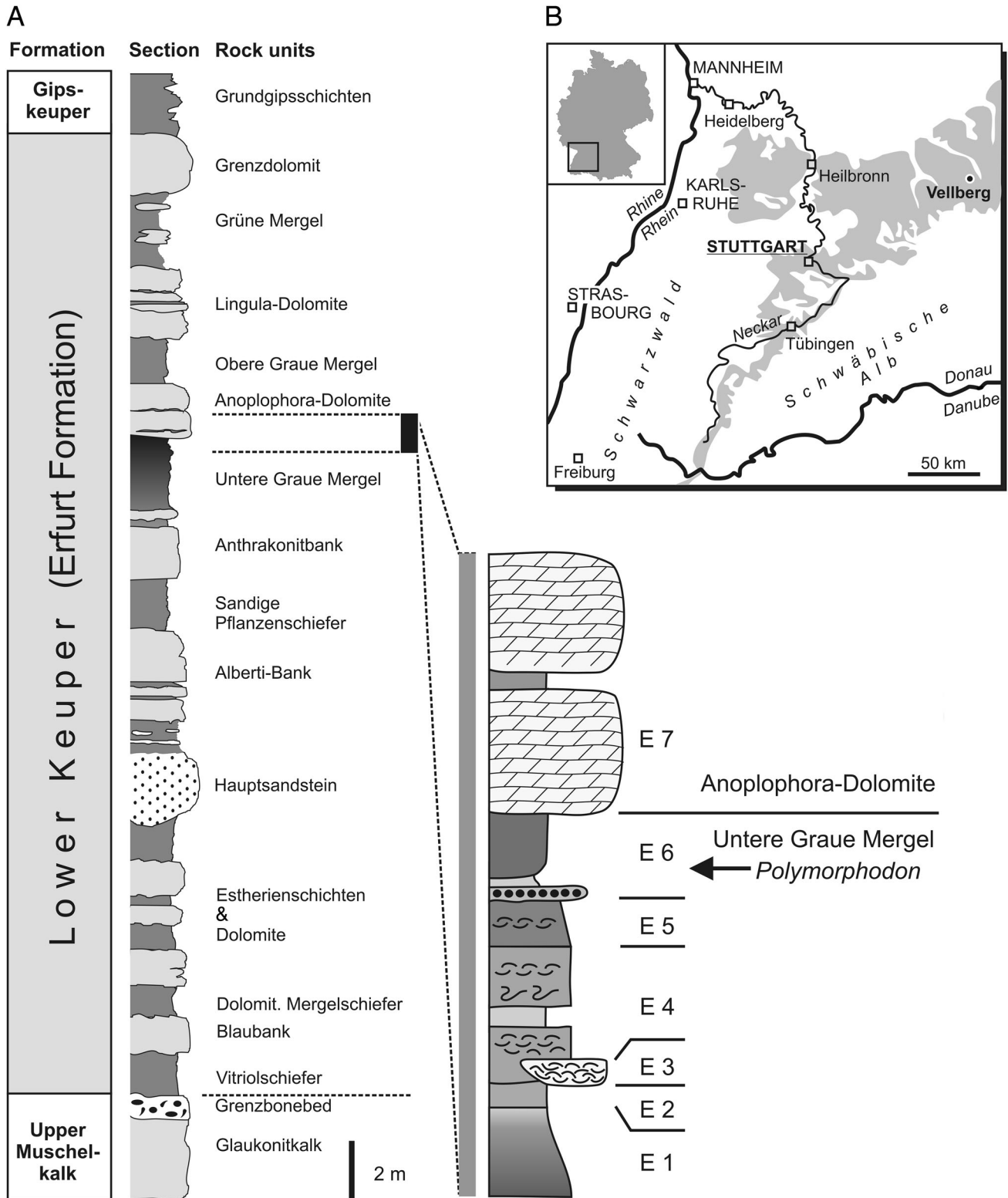


FIGURE 1. **A**, stratigraphic succession of the Erfurt Formation (Lower Keuper; Middle Triassic, Ladinian) in Baden-Württemberg, Germany, with detailed section for the strata exposed in the Schumann quarry near Eschenau. **B**, map of Baden-Württemberg with exposures of Keuper strata in light gray and the location of Vellberg (black dot).

actinopterygian *Dipteronotus* sp., dipnoans, actinistians, and aquatic tetrapods, which comprise a diversity of temnospondyl stem amphibians (*Callistomordax kugleri*, *Gerrothorax pulcherrimus*, *Kupferzelleria wildi*, *Mastodonsaurus giganteus*, *Plagiosuchus pustuliferus*, and

Trematolestes hagdorni). In addition to these apparently autochthonous aquatic elements, the mudstones have also yielded many specimens of terrestrial or semiaquatic tetrapods, including the chroniosuchian stem amniote *Bystrowiella schumanni* (Witzmann

et al., 2008; Witzmann and Schoch, 2018), the enigmatic amniote *Cognathus* sp. (Sues and Schoch, 2013), the paracrocodylomorph pseudosuchian *Batrachotomus kupferzellensis* (which attained a total length of up to 5.5 m; Gower, 1999, 2002; Gower and Schoch, 2009), a basal rhynchocephalian (Jones et al., 2013), the doswelliid archosauriform *Jaxtasuchus salomoni* (Schoch and Sues, 2014), the stem turtle *Pappochelys rosinae* (Schoch and Sues, 2015, 2018a), the stem lepidosaurs *Fraxinisaura rozynekae* (Schoch and Sues, 2018b) and *Vellbergia bartholomaei* (Sobral et al., 2020), and several as yet undescribed diapsid reptiles (Schoch and Seegis, 2016). There are currently few securely dated Ladinian-age occurrences of continental tetrapods known worldwide. Thus, the fossils from the Schumann quarry provide a particularly important record of tetrapod biodiversity during this time interval.

As is the case for most vertebrate fossils from the productive horizon, the two partial skeletons are completely disarticulated, but many bones are preserved in association. Most skeletal elements have been affected by extensive postdepositional compaction. The resulting crushing and flattening of individual bones, often on top of one another, renders identification of many bones and small structural features difficult or currently impossible. Furthermore, pyrite infiltration of bones often prevents detailed imaging using micro-computed tomography (micro-CT) scanning.

The objectives of the present study are to name and diagnose the new taxon of non-archosaurian archosauriforms, document the known material, assess its phylogenetic position among Archosauriformes, and consider the paleobiological implications of its distinctive dentition.

Institutional Abbreviation—SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

Anatomical Abbreviations—**ac**, acetabulum; **adp**, anterodorsal process of premaxilla; **ajp**, anterior process of jugal; **amf**, anterior maxillary foramen; **amp**, anterior process of maxilla; **aof**, antorbital fenestra; **apm**, ascending process of maxilla; **aqj**, articular facet for quadratojugal; **avd**, depression on premaxilla; **bc**, braincase; **bpt**, basipterygoid process; **bt**, basal tuber; **cp**, cultriform process; **cv**, caudal vertebra; **d**, dentary; **djp**, dorsal process of jugal; **en**, external naris; **eo**, exoccipital; **fe**, femur; **fh**, femoral head; **fi**, fibula; **fil**, contact for ilium; **fis**, contact for ischium; **fl**, flange; **fm**, foramen magnum; **fpu**, contact for pubis; **id**, interdental plate; **il**, ilium; **is?**, possible ischium; **j**, jugal; **jp**, jugal (= ventral) process of postorbital; **lc**, lateral condyle; **m**, maxilla; **mc**, medial condyle; **mf**, metotic foramen; **mt**, metatarsal; **mtIV?**, possible metatarsal IV; **mtV**, metatarsal V; **ns**, neural spine; **occ**, occipital condyle; **of**, obturator foramen; **pap**, parietal (= medial) process of postorbital; **pbs**, parabasisphenoid; **pdp**, posterodorsal process of premaxilla; **plp**, palatine portion of pterygoid; **pm**, premaxilla; **po**, postorbital; **poa**, postacetabular process of ilium; **pop**, paroccipital process; **pra**, preacetabular process of ilium; **pt**, pterygoid; **ptf**, pterygoid flange of quadrate; **pu**, pubis; **q**, quadrate; **qfl**, quadrate flange of pterygoid; **qh**, proximal head of quadrate; **so**, supraoccipital; **sqp**, squamosal (= posterior) process of postorbital; **ti**, tibia; **tp**, transverse process (= caudal rib); **vpo**, ventral process of opisthotic.

METHODS

The holotype was micro-CT-scanned at the Zeiss Metrology Services facility in Aalen, Germany. Scanning was performed on a Zeiss Metrotom micro-CT scanner without a filter and with a voltage of 100 kV. The resolution ranged from 23 to 30 μm . The bones were digitally segmented with Amira 6.1 and rendered with the Volren option, and the images were finally processed in Adobe Photoshop.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903, sensu Gauthier, Kluge, and Rowe 1988

ARCHOSAURIFORMES Huene, 1946, sensu Benton, 1985

ARCHOSAURIFORMES Gauthier, Kluge, and Rowe 1988

EUCROCOPODA Ezcurra, 2016

POLYMORPHODON ADORFI, gen. nov., sp. nov.
(Figs. 2–8)

Holotype—SMNS 91343, disarticulated partial skeleton preserved on three blocks of mudstone (Fig. 2). Identifiable elements include a partial left premaxilla (concealed in matrix), both maxillae, left frontal, right postorbital, left jugal (concealed in matrix), both quadrates, occipital portion of braincase, incomplete parabasisphenoid, partial right and nearly complete left pterygoid, fragments of possible vomers, partial dentaries, caudal vertebrae, complete left and fragment of right ilium, left ?ischium, pubis, left femur, left tibia, possibly left fibula, two metatarsals, and other autopodial elements. There appear to be no other associated tetrapod remains; thus, the aforementioned bones likely represent a single individual.

Referred Specimen—SMNS 91400, two blocks of mudstone preserving a small set of disarticulated skeletal elements including a left premaxilla (Fig. 3A), incomplete left maxilla, partial right jugal, fragment of right dentary, partial braincase, left pterygoid, and teeth.

Etymology—From Greek *polys*, many, *morphe*, shape, and *odon* (form of *odous* used in composites), tooth, in reference to the distinctly heterodont dentition. The species name honors Norbert Adorf, preparator at the Staatliches Museum für Naturkunde Stuttgart, whose dedicated efforts in field work and preparation have helped the museum build its extensive collections of Triassic vertebrate fossils from Baden-Württemberg during the past 30 years.

Locality and Horizon—Schumann limestone quarry, southeast of Eschenau, in the municipality of Vellberg, Baden-Württemberg, Germany. Untere Graue Mergel (unit E6c–d; Schoch and Seegis, 2016), Lower Keuper (Erfurt Formation); upper Middle Triassic (Ladinian, Longobardian).

Diagnosis—Slender-limbed, small archosauriform diagnosed by the following craniodental autapomorphies: (1) premaxilla with long, leaf-shaped posterodorsal process that is slightly longer than body of element; (2) premaxilla with deep lateral fossa anteroventral to external narial fenestra; (3) premaxilla with five conical, gently recurved teeth; (4) mesial and distal carinae of labiolingually flattened maxillary and dentary tooth crowns with large, somewhat hook-shaped denticles aligned at distinct angle to apicobasal axis of tooth crown; and (5) presence of ledge on medial surface of maxilla above interdental plates.

Polymorphodon adorfi differs from a second, as yet undescribed taxon of non-archosaurian archosauriform from the same horizon and locality in features of the dentition and the absence of fine sculpturing on the cranial bones (Irmis and Schoch, unpubl. data).

Polymorphodon adorfi differs from the doswelliid archosauriform *Jaxtasuchus salomoni* from same horizon and locality in the structure of the tooth crowns, which in the latter are slender, conical, and covered with apicobasal ridges on the labial and lingual surfaces and have smooth carinae, and the proportions of the cranium (Schoch and Sues, 2014).

DESCRIPTION

Skull

None of the available cranial and mandibular bones bears external sculpturing. The reconstructed cranium is fairly deep dorsoventrally, and the snout is not elongated (Fig. 7C). The external nares are located at the anterior end of the snout and face laterally. An antorbital fenestra is present, but the presence of an antorbital fossa remains uncertain (see below). The

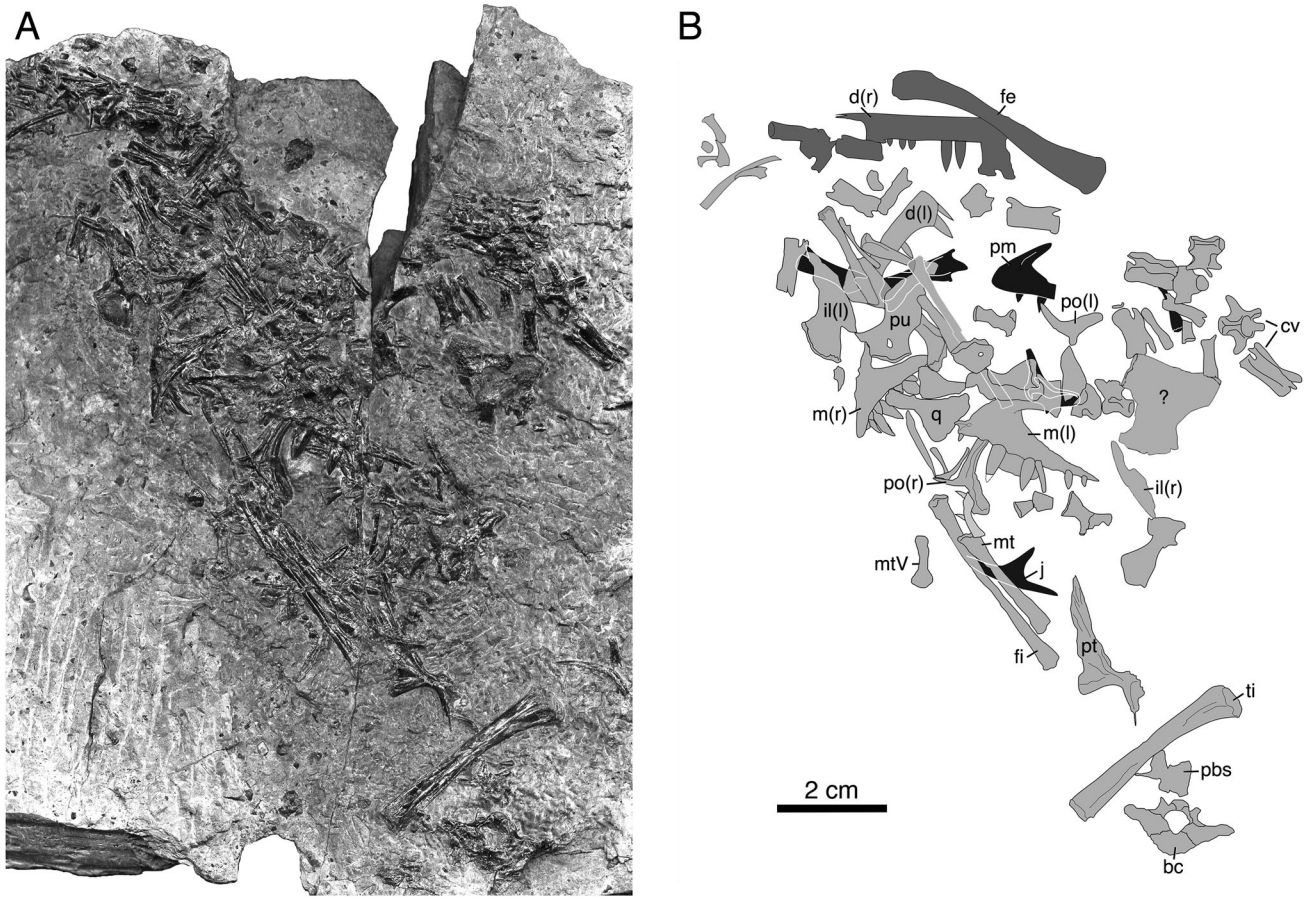


FIGURE 2. *Polymorphodon adorfi*, gen. et sp. nov., partial skeleton (SMNS 91343, holotype). **A**, photograph of main block and **B**, explanatory diagram with labels for identified skeletal elements. The diagram also includes elements exposed on a partial counterpart (at the top of the illustration; inverted and highlighted in dark gray). Bones visible only on micro-CT scans are rendered in black. For abbreviations in the figures, see text; '(l)' and '(r)' denote left and right elements, respectively, of several bones.

triradiate shape of the postorbital indicates the presence of separate infra- and supratemporal fenestrae. We estimate the length of the skull of SMNS 91343 to be about 60 mm. For comparison, the reconstructed skull of *Osmolskina czatkowicensis* has the same estimated length (Borsuk-Białynicka and Evans, 2009) and the skull of the holotype of *Euparkeria capensis* has a midline length of 78.8 mm (Ewer, 1965).

Premaxilla—The premaxilla is represented by a complete left element in SMNS 91400 (greatest length: 15 mm; Fig. 3A) and an only partially exposed incomplete left bone in SMNS 91343. Its robust body holds five teeth. This number is shared with *Erythrosuchus africanus* and *Vancleavea campi*, but *E. capensis* and *O. czatkowicensis* each have four premaxillary teeth (Gower, 2003; Borsuk-Białynicka and Evans, 2009; Nesbitt et al., 2009; Sookias, 2016). The anterior three premaxillary teeth have tall, conical, and slightly recurved crowns that lack carinae. The second tooth is the tallest of the anterior three. There is a space for a fourth tooth, and a small and slender fifth tooth is situated at the posterior end of the alveolar margin of the premaxilla. The anterodorsal (= prenarial) process extends posterodorsally and is slightly set back from the somewhat bulbous anterior end of the premaxillary body. Just behind the base of this process, the premaxilla forms a deep depression ventral to the external naris and bounded ventrally by the thick alveolar margin and posteriorly by the posterodorsal process of the premaxilla. The posterodorsal (= postnarial) process is plate-like and slightly longer

than the anteroposterior length of the body of the premaxilla. It has a dorsoventrally deep, leaf-shaped outline in lateral view, increasing in depth from its junction with the body of the premaxilla and then tapering again more posteriorly. The posterodorsal process resembles those in Proterosuchidae and Erythrosuchidae (Ezcurra, 2016) and differs from the short, nearly vertical lappet in *E. capensis* (see Ewer, 1965). It articulated with the maxilla (and possibly the nasal) and excluded the former from participation in the posterior margin of the external naris. A dorsal flange at the base of the posterodorsal process formed the posteroventral margin of the external naris as in *Archosaurus rossicus*, *Proterosuchus* spp., *Sarmatosuchus otschevi*, and some specimens of the erythrosuchid *Garjainia madiba* (e.g., Ezcurra, 2016).

Maxilla—Both maxillae are preserved in SMNS 91343, the nearly complete left bone (length: 34 mm) exposed in lateral view (Fig. 3B) and the slightly distorted, less complete right element exposed in medial view (Fig. 3C). In addition, much of a left maxilla is exposed in medial view in SMNS 91400. The mediolaterally flattened maxilla is more than twice as long anteroposteriorly as tall dorsoventrally. It has a short anterior process, a posterodorsally tapering dorsal (= ascending) process, and a posteriorly tapering posterior process. The portion of the maxilla anterior to the anterior margin of the antorbital fenestra is much shorter than that behind the anterior margin of that opening, as in other non-archosaurian archosauriforms and basal archosaurs (Nesbitt, 2011). The anterior process of the

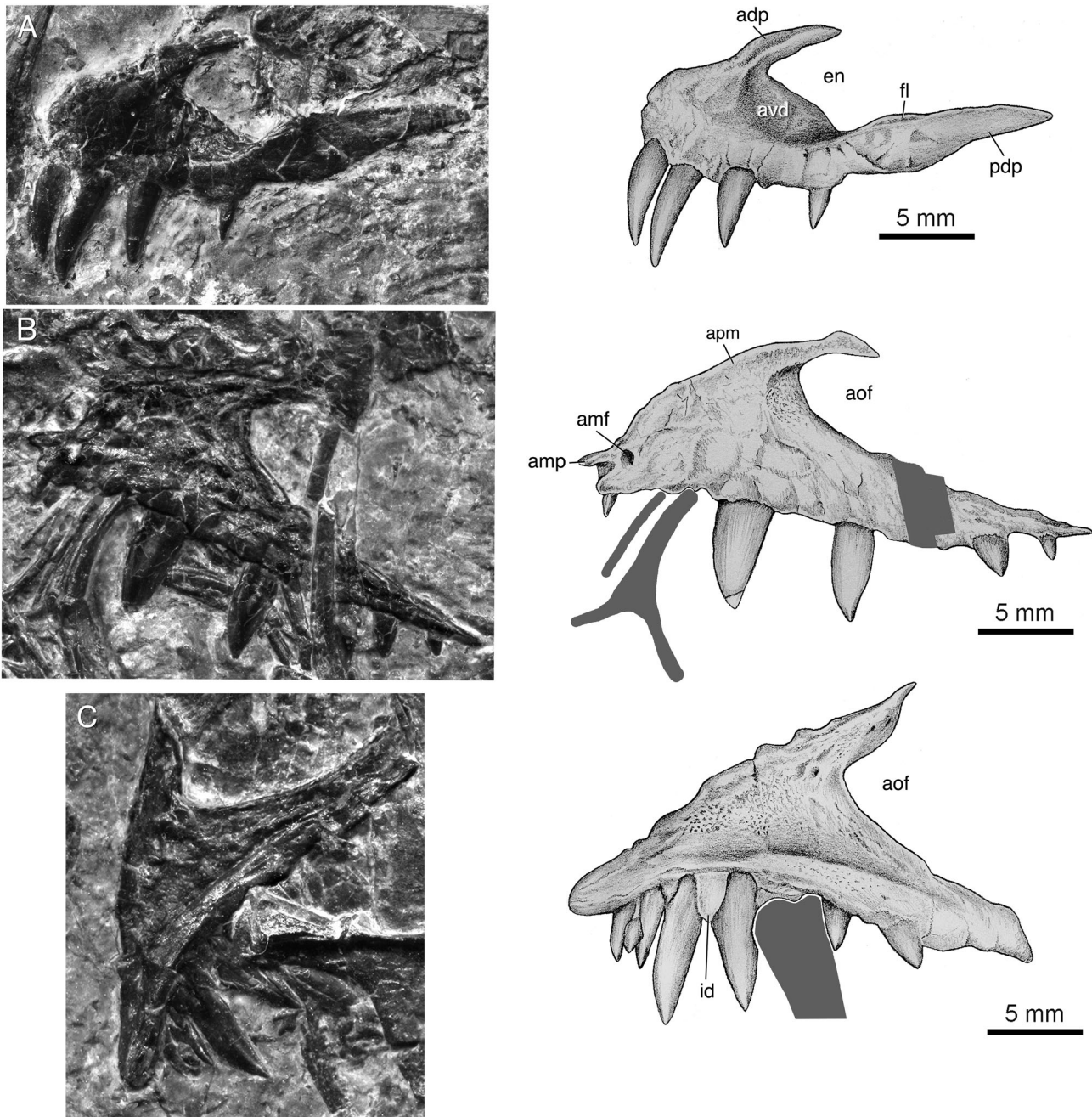


FIGURE 3. *Polymorphodon adorfi*, gen. et sp. nov. **A**, left premaxilla (SMNS 91400) in lateral view. **B**, left maxilla (SMNS 91343, holotype) in lateral view. **C**, right maxilla (SMNS 91343, holotype) in medial view. Gray areas represent overlying bones.

maxilla curves gently anteroventrally and is separated from the anterior end of the alveolar margin by a small, anteriorly facing notch. It presumably contacted the medial surface of the premaxilla. Posterolateral to the process, an opening on the lateral surface of the maxilla corresponds to the anterior maxillary foramen (for the supraalveolar canal) in non-archosauriform archosauromorphs (e.g., *Prolacerta broomi*; Modesto and Sues, 2004) and in other non-archosaurian archosauriforms (e.g., *O. czatkowicensis*; Borsuk-Białynicka and Evans, 2009). The posterior process of the maxilla rapidly tapers posteriorly and presumably terminated below the orbit. It bears an oblique dorsal facet for contact with the anterior process of the jugal. A

posteriorly tapering posterior process is considered the plesiomorphic condition for archosauriforms (Ezcurra, 2016). Although it is difficult to delineate its extent due to crushing, a shallow antorbital fossa appears to be present at the base of the dorsal process of the left maxilla in SMNS 91343. A narrow recess is located at the rounded anterior end of the antorbital fenestra on the medial surface of the bone. The medial surface of the right maxilla of SMNS 91343 bears an obliquely dorsomedially facing ledge, which extends just above the interdental plates posteriorly up to the level of the anterior end of the antorbital fenestra where it changes to a thickened ridge. There is no clearly defined area for contact with the palatine. More anteriorly, the

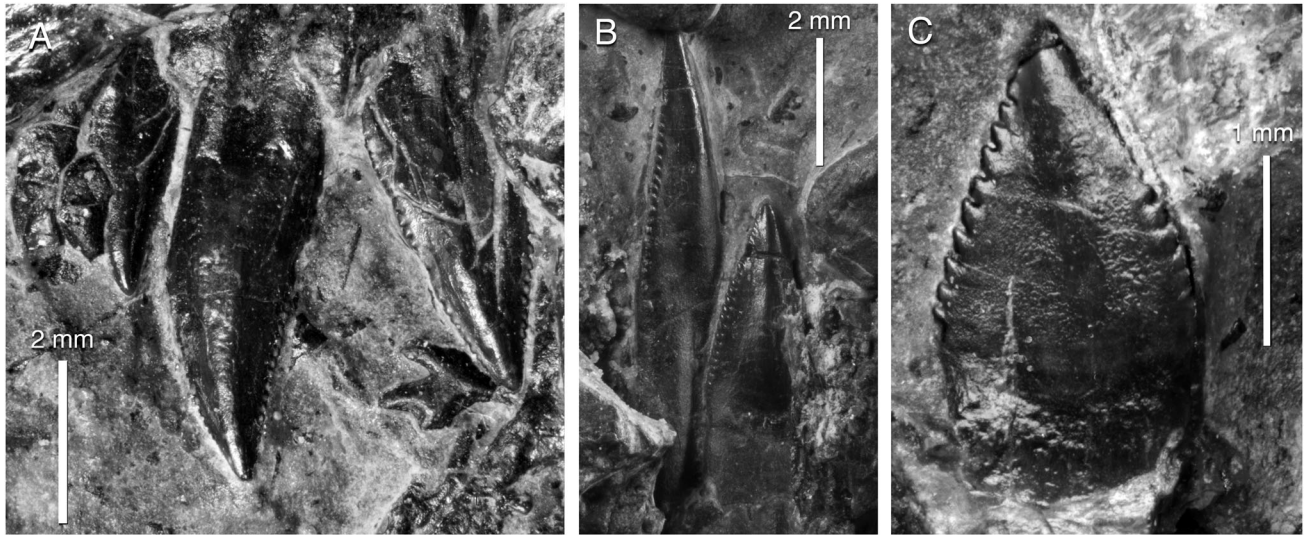


FIGURE 4. *Polymorphodon adorfi*, gen. et sp. nov., teeth in labial view. **A**, anterior teeth from a left maxilla (SMNS 91343, holotype). **B**, two dislodged anterior teeth from a right dentary (SMNS 91343, holotype). **C**, posterior tooth from a left dentary (SMNS 91400).

ledge turns into an obliquely dorsomedially facing palatal shelf. However, the medial surface of the left maxilla of SMNS 91400 bears a slightly thickened ridge rather than a ledge. The dorsal process of the maxilla is long and probably tapering (being damaged or concealed by overlying bones near the dorsal ends on the available maxillae). It is aligned at an angle of about 45° to the alveolar margin. The medial surface of the process bears scattered tiny foramina.

Based on the left element of SMNS 91343, the maxilla had at least 11 tooth positions. *Euparkeria capensis* and *O. czatkowiczensis* each have 13 maxillary teeth (Borsuk-Białynicka and Evans, 2009). The maxillary tooth row extends close

to the posterior end of the bone. The alveolar margin of the left maxilla of SMNS 91343 is rather straight. Unlike those of the premaxilla, the crowns of the maxillary teeth are labiolingually flattened and have distinct carinae. In transverse section, they are oval at the base but become lenticular in section toward the apex. The height of the tooth crowns reaches its maximum just anterior to the midpoint of the maxillary tooth row. The first maxillary tooth on the left maxilla and the anterior two or possibly three teeth on the right element of SMNS 91343 are small (Figs. 3B, C, 4A). On the left maxilla, the second tooth is taller than the first but less robust than the teeth behind it. The posterior maxillary tooth crowns are shorter and less pointed. Crown heights range from 1.5 to 7 mm. The shape of the tooth crowns ranges from asymmetrical with variously recurved apices (and a convex mesial and a straight or gently concave distal carina) to symmetrically lanceolate (on the more posterior teeth). All tooth crowns have distinctly serrated mesial and distal carinae (with 6 or 7 serrations per mm) (Fig. 4A). The proportionately large serrations (denticles) are somewhat hook-shaped and aligned at a distinct angle to the apicobasal axis of the tooth crown rather than perpendicular to the carina. They are typically restricted to the more apical portion of the mesial carina, whereas those along the distal carina extend close to the base of the crown. Both the mesial and distal serrations decrease in size toward the apex of the tooth crown. The roots of the teeth are long, and no constriction or 'neck' separates the crown from the root. Tooth implantation is thecodont. Individual teeth are separated lingually by broad and tall interdental plates, which are not fused to each other and are inset from the remainder of the lingual surface of the maxilla.

Frontal—The left frontal of SMNS 91343 is visible in dorsal view on micro-CT scans, but it is heavily infiltrated by pyrite and thus shows little detail except for the slightly thickened orbital rim. It is rather broad transversely at its anterior and posterior ends.

Postorbital—Most of the right postorbital is exposed in medial view next to the alveolar margin of the left maxilla in SMNS 91343 (Fig. 5A). It formed the posterodorsal margin of the orbit, much of the dorsal and anterior borders of the infratemporal fenestra, and the anterolateral margin of the supratemporal opening. The postorbital is triradiate, with the processes extending at nearly right angles to each other. The medial process is

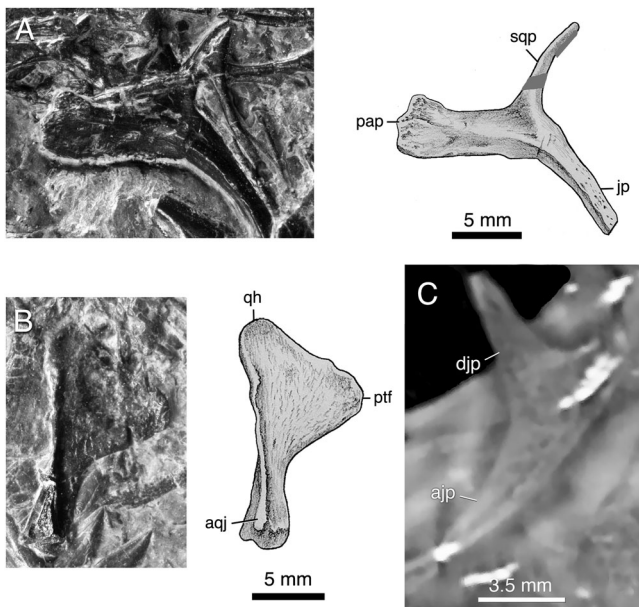


FIGURE 5. *Polymorphodon adorfi*, gen. et sp. nov., cranial bones (SMNS 91343, holotype). **A**, right postorbital in medial view. **B**, right quadrate in lateral view. **C**, left jugal in lateral view (micro-CT scan image).

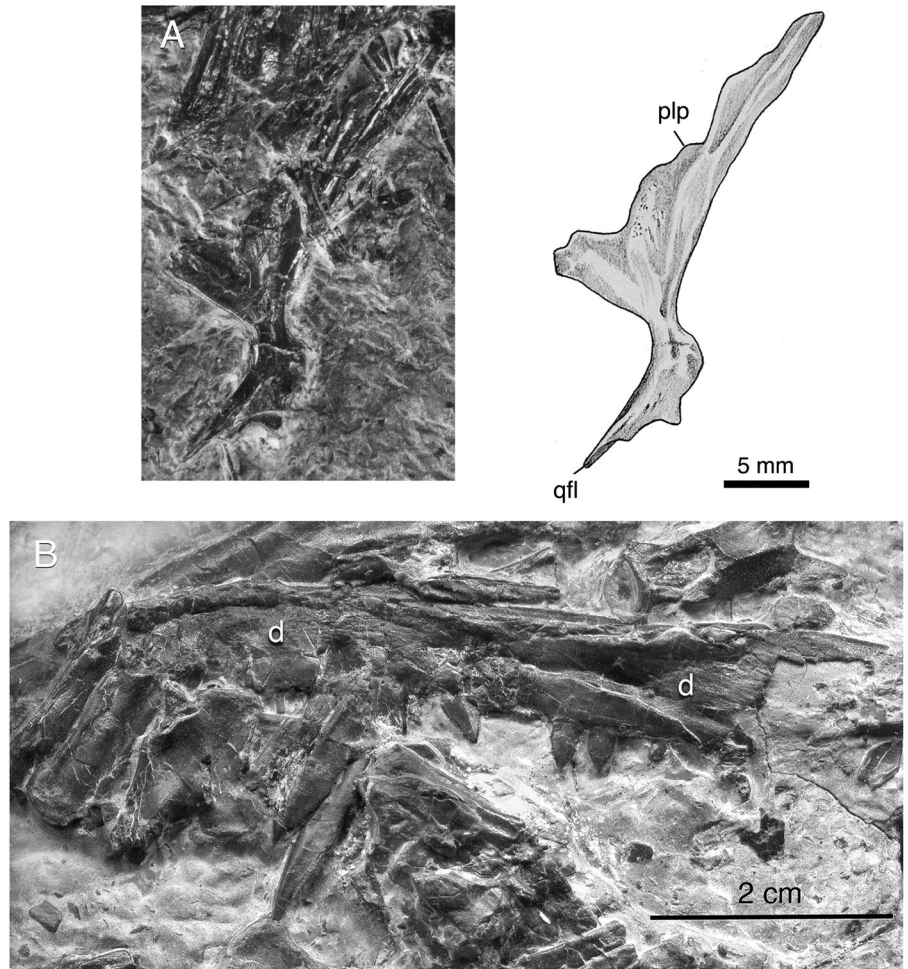


FIGURE 6. *Polymorphodon adorfii*, gen. et sp. nov., skull bones (SMNS 91343, holotype). **A**, left pterygoid in dorsal view. **B**, right dentary (with associated postcranial bones).

broad, and its blunt medial end forms a facet for contact with the parietal. The slender posterior process curves posterodorsally and presumably inserted into a slot on the lateral surface of the squamosal. The ventral process of the postorbital is long and gently curved anteroventrally. Its distal end is not exposed. The medial side of the postorbital bears a pronounced ridge, which extends from the medial end of the medial process to the distal end of the ventral process.

Jugal—A fragment of a right jugal is exposed in lateral view in SMNS 91400. Its lateral surface bears slight, irregular sculpturing and a ventrolateral surface for contact with the maxilla anteriorly. A more complete left jugal is preserved close to the right maxilla in SMNS 91343 but is only visible on micro-CT scans (Fig. 5C). It is triradiate and mediolaterally flattened. The anterior process of the jugal forms the ventral margin of the orbit. It is dorsoventrally deep near the junction of the three processes and curves gently anterodorsally, forming a gently concave ventral margin of the orbit. The dorsal process of the jugal is slightly posterodorsally inclined and straight. It forms part of the anterior margin of the infratemporal fenestra and the posteroventral margin of the orbit. The posterior process is dorsoventrally deep close to the junction of the three processes. It appears to be the shortest of the processes and probably formed much of the ventral border of the infratemporal opening.

Quadrate—A complete right quadrate (dorsoventral height: 19 mm; Fig. 5B) is exposed in lateral view overlying teeth the

right maxilla of SMNS 91343. It has a more or less triangular pterygoid flange, which occupies about half of the total dorsoventral height of the element. The rounded proximal head for contact with the squamosal is not offset. A thin anterolateral crest extends from the proximal end of the quadrate to its distal trochlea. It has a triangular lateral thickening at its distal end for contact with the quadratojugal (which is not preserved). As in other non-archosaurian archosauriforms (Nesbitt, 2011), the quadrate probably extended posteroventrally in life. It is straight posteriorly and, in this respect, resembles the quadrates of other non-archosaurian archosauriforms such as *Er. africanus* rather than the recurved quadrates of *Doswellia kaltenbachi* and *V. campi* (Gower, 2003; Dilkes and Sues, 2009; Nesbitt et al., 2009).

Pterygoid—A nearly complete left pterygoid (Fig. 6A) exposed in dorsal view and part of the right element are preserved in SMNS 91343 and an incomplete left pterygoid in SMNS 91400. The long palatal portion of the pterygoid is narrow transversely for most of its length. Because the ventral surface is not exposed on any of the available elements, it cannot be ascertained whether the pterygoid bore teeth or denticles. A constriction separates the palatal portion of the pterygoid from the thin, posterolaterally extending flange for contact with the quadrate. The recess for the reception of the basiptyergoid process on the medial surface of the pterygoid is not exposed on any of the available elements.

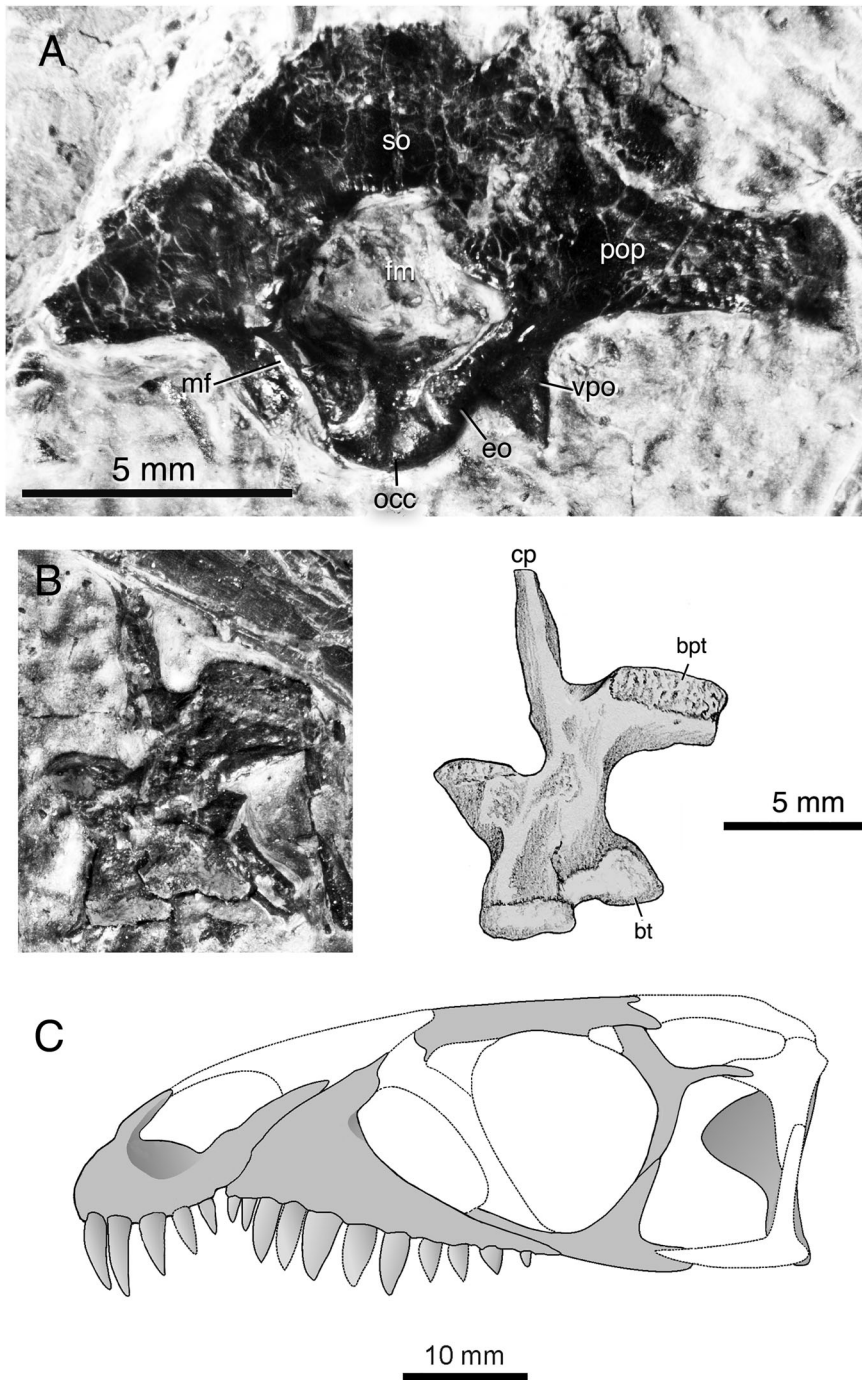


FIGURE 7. *Polymorphodon adorfii*, gen. et sp. nov., braincase. **A**, partial braincase (SMNS 91343, holotype) in occipital view. **B**, parabasi-sphenoid in ventral view. **C**, simplified reconstruction of the cranium in left lateral view. Preserved bones are highlighted in gray. The presence of a small antorbital fossa just anterior to the terminus of the antorbital fenestra is uncertain.

Vomer—Two fragments of rod-like bones in SMNS 91343, bearing small recurved teeth, possibly represent vomers.

Braincase—Much of the occipital surface of the braincase is exposed on the main block of SMNS 91343 (Fig. 7A), but the quality of preservation obscures many details. A partial, poorly preserved braincase is preserved in anterior view in SMNS 91400. The large, plate-like supraoccipital is slightly inclined anterodorsally and forms the dorsal margin of the foramen magnum. The occipital condyle is mostly formed by the basioccipital except for the dorsolateral corners, which are contributed by the exoccipitals. It lacks a distinct ‘neck’ that would offset it from the

occipital surface of the basicranium. The posterior surface of the occipital condyle bears a shallow notochordal pit. Its dorsal margin is slightly concave along the ventral margin of the foramen magnum. Unlike in Erythrosuchidae (Gower and Sennikov, 1996) but as in *E. capensis*, *O. czatkowicensis*, and *D. kaltenbachi* (Borsuk-Białynicka and Evans, 2009; Dilkes and Sues, 2009; Sobral et al., 2016), the basioccipital separates the expanded ventral ends of the exoccipitals on the transversely concave ventral floor of the endocranial cavity. The facets for contact with the exoccipitals face obliquely laterally. In the area anterior to each facet, a narrow fissure represents the metotic

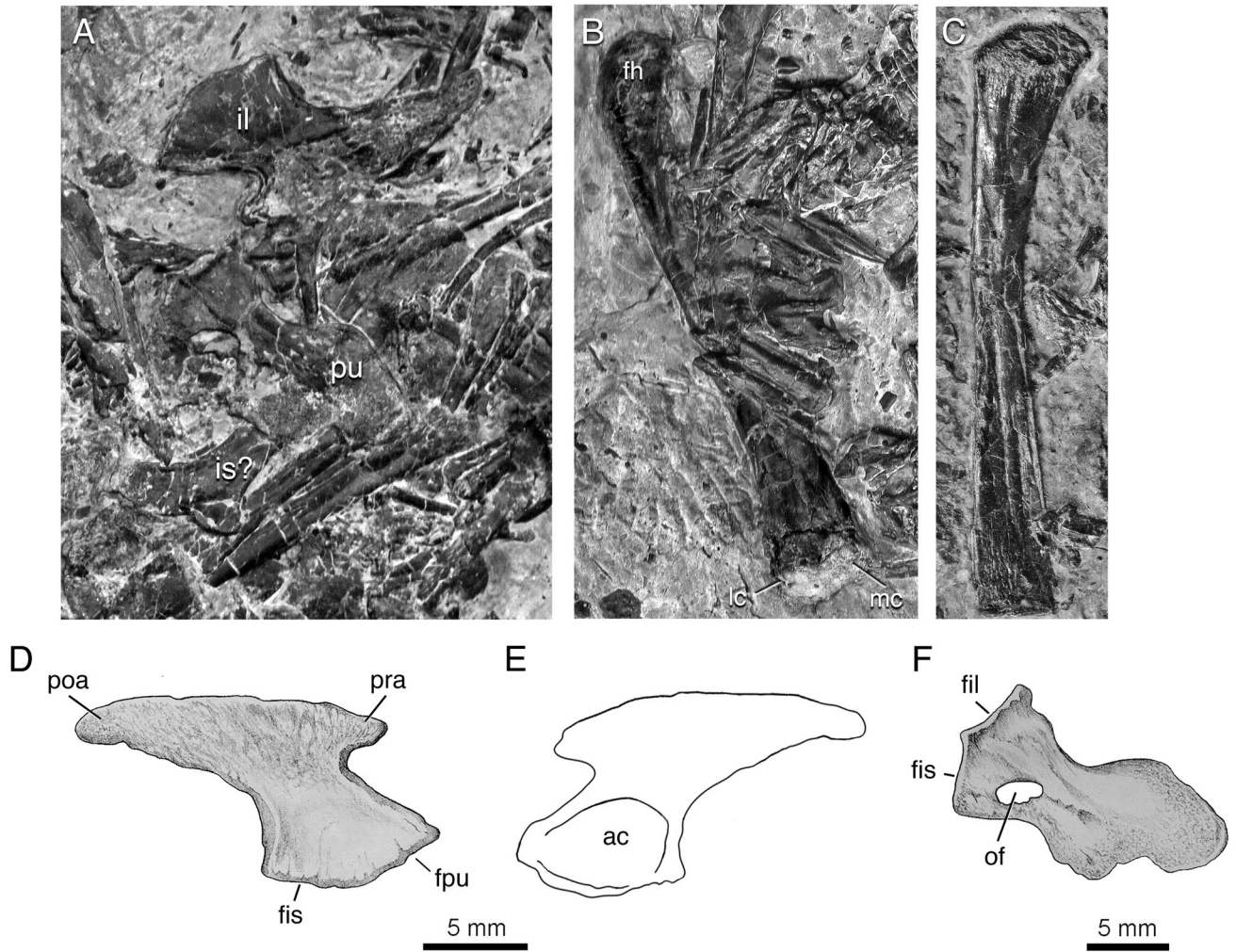


FIGURE 8. *Polymorphodon adorfi*, gen. et sp. nov., pelvic elements, femur, and tibia (SMNS 91343, holotype). **A**, pelvic bones as preserved. **B**, left femur in ventral view; length of femur: 43 mm. **C**, left tibia in lateral view; length of tibia: 38 mm. **D**, **E**, left ilium in **D**, medial view and **E**, outlined in lateral view (traced from a micro-CT image). **F**, pubis.

foramen. This fissure is dorsoventrally elongate, extending up to the base of the paroccipital process, as in *E. capensis* (e.g., Sobral et al., 2016). A small anterior projection located at mid-height of the exoccipital on both sides suggests that this opening was slightly constricted at this point. The medial surface of each exoccipital close to the margin of the foramen magnum has a narrow opening, which possibly represents the metotic foramen and the exit for the hypoglossal nerve (cranial nerve [CN] XII). There are no visible lateral foramina for CN XII on either side. Two damaged areas on the medial surfaces of these exoccipitals possibly include the medial entrances of these nerves. There is no obvious sutural separation between the exoccipital and the opisthotic, but it is likely that most of the paroccipital process was formed by the latter bone, as in *E. capensis* (e.g., Sobral et al., 2016). The paroccipital process projects somewhat posterolaterally. It is flat anteroposteriorly and slightly expanded at its dorsoventrally convex distal end (SMNS 91400). The well-developed ventral ramus of the opisthotic extends laterally well beyond the lateral-most edge of the exoccipital in occipital view, as is typical for archosauriforms (Gower, 2002).

Much of a crushed parabasisphenoid (including the posterior portion of the cultriform process; Fig. 7B) is exposed in ventral

view between the left tibia and the partial braincase in SMNS 91343. It is plate-like and extends horizontally, as in *Proterosuchus fergusi* and unlike the vertical alignment in *Er. africanus* (Cruickshank, 1972; Gower and Sennikov, 1996). The parabasisphenoid was not fused to the basioccipital. Anterior to the ventrolateral crests, the parabasisphenoid decreases in transverse width. Little detail is evident for the basal tubera, but they appear to be separated. The robust basiptyergoid process (best preserved on the left side) extends anterolaterally and forms a broad facet for contact with the pterygoid. No foramina for the entrance of the cerebral branches of the internal carotid arteries are evident on the ventral surface of the parabasisphenoid.

Dentary—Parts of both dentaries are preserved in lateral view in SMNS 91343, and a fragment of a right dentary is visible in medial view in SMNS 91400. The mediolaterally flattened and dorsoventrally low tooth-bearing rami have more or less parallel dorsal (alveolar) and ventral margins. The left dentary of SMNS 91343 appears to show a slight increase in dorsoventral depth near the anterior end, but the condition in SMNS 91400 is not clear. Anteriorly, the ventral margin of the dentary curves anterodorsally. The symphysis was presumably restricted to the anterior end of the bone. The more complete but badly crushed right dentary of SMNS 91343 (Fig. 6B) has two anterior teeth (which

slipped from their alveoli) with tall, straight crowns (Fig. 4B) and all other teeth with short, symmetrical crowns (Fig. 4C). The distinct interdental plates are slightly inset from the remainder of the medial surface of the dentary and not fused to each other. The presence of an external mandibular fenestra cannot be ascertained based on the available dentaries.

Postcranial Skeleton

Vertebral Column—A number of scattered vertebrae are preserved in both SMNS 91343 and SMNS 91400, but preservation renders identification and observation of details difficult in many cases. All vertebrae have amphicoelous centra with anteroposteriorly concave sides and lacking notochordal perforations. Where the condition can be ascertained, the vertebrae lack neurocentral sutures, suggesting skeletal maturity of the specimens.

Most of the identifiable vertebrae are caudals (Fig. S1). A proximal caudal vertebra has large, slightly posterolaterally curved and tapering transverse processes that are completely fused to the vertebra. Its short, spool-shaped centrum has beveled anterior and posterior edges. More distal caudal vertebrae have more mediolaterally compressed and elongate centra, which are surmounted by dorsoventrally low neural arches with slender pre- and postzygapophyses. The more proximal of these vertebrae have a low neural spine that forms a posteriorly projecting point. The neural spines disappear on the more distal caudals.

Manus—Carpal elements are likely present but cannot be unequivocally identified. Probable metacarpals and manual phalanges indicate a proportionately small and gracile manus. The phalanges show differences in length and robustness, but they cannot be confidently assigned to particular digits in the absence of articulated remains.

Several ungual phalanges of various sizes are preserved in SMNS 91343, but they cannot be definitely assigned to either manus or pes. All are mediolaterally flattened and moderately curved, terminating in pointed tips distally. Each ungual bears a ventral flexor tubercle just distal its proximal articular surface.

Ilium—The complete left ilium (Fig. 8A, D, E) and the dorsal margin as well as a faint impression of the right element are preserved in SMNS 91343. The former is exposed in medial view. The dorsal margin of the low iliac blade is slightly convex anteroposteriorly. The triangular postacetabular process is long, equivalent to half the anteroposterior length of the ilium (17 mm) and distinctly longer than deep dorsoventrally. Its posterior end is rounded, and its ventral margin is slightly concave anteroposteriorly. The pointed preacetabular process is much shorter anteroposteriorly. It is also short in *Erythrosuchus africanus* and *Euparkeria capensis*, but *Proterosuchus* spp. lacks this process altogether (Ewer, 1965; Cruickshank, 1972; Gower, 2003). The acetabular portion of the ilium is separated from the dorsal blade by a slight constriction at the level of the dorsal margin of the laterally facing acetabulum. CT scans revealed that the acetabulum has a more or less rounded outline and lacks a prominent supraacetabular buttress. The ventral margin of the acetabular portion of the ilium has equally long areas for contact with the pubis and the ischium, respectively. The distance between these articular areas is slightly more than half of the total length of the iliac blade.

Pubis—We interpret a large, plate-like bone (Fig. 8A, F) in the region of the antorbital fenestra of the right maxilla in SMNS 91343 as a pubis. Based on this interpretation, the proximal end of the element has two contact surfaces for the ilium and the ischium, respectively, which are set at an angle to each other. A large, oval opening close to the proximal end represents the obturator foramen. The distal portion ('apron') of the bone is distinctly expanded and set off from the proximal region by a

constriction. Due to the inadequate preservation, it is uncertain whether this bone represents the left or right pubis.

Adjacent to the right ilium in SMNS 91343 are poorly preserved fragments of a plate-like bone, which possibly represents an ischium or a pubis.

Ischium—A flattened bone (Fig. 8A) adjacent to the pubis and the right maxilla of SMNS 91343 possibly represents the proximal portion of an ischium. Again, it is not clear whether it represents the left or right element. The proximal end of this bone is divided into a thicker, broader dorsal portion for contact with the pubis and a distinct anterior process for contact with the pubis. The exposed portion of the shaft is rather straight and, with the exception of a thickened dorsal edge, flat.

Femur—A complete but dorsoventrally crushed left femur is exposed in ventral view in SMNS 91343 (Fig. 8B). It is 43 mm long and has an only slightly sigmoid curvature. The indistinct, medially turning proximal head of the femur is not offset from the shaft. On the proximal portion of the femur, a low ventral ridge near the medial margin probably served for the insertion of *M. caudifemoralis* as in other archosauriforms (Nesbitt, 2011). Crushing in this region makes it difficult to delineate this feature. The somewhat expanded distal end of the femur (width: 7 mm) has slightly separated, ventrally facing condyles, which do not project much beyond the shaft.

Tibia—SMNS 91343 preserves the left tibia exposed in lateral view (Fig. 8C). The bone is shorter than the femur (38 mm; 88% of femoral length) and slightly sigmoid. Its proximal end is expanded and slightly convex. The less expanded distal articular end of the tibia is continuous with the shaft and shows little detail. Although the condition was likely accentuated by postmortem crushing, the tibial shaft apparently had an oval outline in transverse section with the long axis aligned anteroposteriorly.

The lengths of the femur and the tibia closely correspond to those of the homologous elements in *Osmolskina czatkowicensis*, for which Borsuk-Białynicka and Sennikov (2009) reported modal lengths of about 40 and 30 mm, respectively.

Fibula—A complete, possibly left fibula is preserved in SMNS 91343 (Fig. S2). It is as long as the tibia (38 mm) and has slightly expanded proximal and distal ends. The shaft of the fibula is much less robust than that of the tibia.

Pes—A well-preserved left metatarsal V (length: 9.7 mm) is exposed in plantar view in SMNS 91343 (Fig. S2). It is short and robust, with an expanded proximal end that gradually curves medially, as in *E. capensis* and *Parasuchus hislopi* (e.g., Ezcurra, 2016). Another metatarsal is partially exposed next to the fibula in SMNS 91343 (Fig. S2). It is slender and straight, with an estimated length of about half that of the femur; based on its relative length, it is possibly metatarsal IV.

As is the case for the carpus and manus, various disassociated bones are likely attributable to the tarsus and pes but, in the absence of articulated feet, they cannot be identified more precisely.

Dermal Armor—Neither of the two specimens preserves any osteoderms. Because many other skeletal elements, especially from the postcranial axial skeleton, are also missing, this is presumably a taphonomic artifact. Based on the phylogenetic position of *Polymorphodon adorfi*, it is likely that it had small dorsal osteoderms, which could have easily drifted away during the postmortem disintegration of the animal's body.

PHYLOGENETIC POSITION OF *POLYMORPHODON*

Polymorphodon adorfi can be referred to Archosauriformes based on the presence of two diagnostic unambiguous synapomorphies listed by Nesbitt (2011) for this clade: (1) presence of an antorbital fenestra (Fig. 7C) and (2) presence of mesial and distal tooth serrations. Furthermore, it shares two features of the ilium that Ezcurra et al. (2010) considered diagnostic for

Archosauriformes: (1) presence of a slightly convex or straight dorsal margin of the iliac blade and (2) an iliac blade with a greatest length more than three times greater than its maximum height (Fig. 8D, E). The latter authors also cited the presence of a distinct preacetabular process and the inclusion of an angle more acute than 45° between the long axis of the ilium and the dorsal margin of its pubic portion as archosauriform features. Again, *P. adorfi* shares both character states.

The presence of well-developed interdental plates (Fig. 3C) places *P. adorfi* closer to crown-group archosaurs because this feature is absent in the non-archosauriform archosauromorph *Prolacerta broomi* and basal archosauriforms such as *Proterosuchus* spp. and *Erythrosuchus africanus* (Gower, 2003; Modesto and Sues, 2004; Ezcurra and Butler, 2015). However, the more derived archosauriforms *Euparkeria capensis* and *Osmolskina czatkowiczensis* both have well-developed interdental plates (Ewer, 1965; Borsuk-Białynicka and Evans, 2009). *Polymorphodon adorfi* has a posteriorly tapering posterior process of the maxilla ventral to the antorbital fenestra (Fig. 3B), which differs from the condition in more basal archosauriforms such as *Proterosuchus* spp. and *Er. africanus* (Gower, 2003; Ezcurra and Butler, 2015).

In order to assess the phylogenetic position of *P. adorfi*, we used the character-taxon matrix compiled by Ezcurra (2016) because it is based on a broad range of diapsid taxa including most known non-archosaurian archosauriforms and has a comprehensive list of cranial and postcranial features. We added the character states for the new taxon (Appendix 1; Supplemental Data in Correction <http://dx.doi.org/10.1080/02724634.2020.1791513>) and were able to score it for 169 out of a total of 600 characters (28.17%). First, the modified matrix was analyzed with equally weighted parsimony using TNT 1.1 (Goloboff et al., 2008). A heuristic search of 1,000 replications of Wagner trees (random addition sequence) was followed by the application of the tree bisection and reconnection (TBR) branch-swapping algorithm (holding 10 trees per replicate). Our analysis recovered eight most parsimonious trees, each with a length of 2,663 steps, a consistency index (CI) of 0.296, and a retention index (RI) of 0.609. The strict consensus of these trees is illustrated in Figure 9.

The overall tree topology is the same as that recovered by Ezcurra (2016). The analysis found *P. adorfi* in an unresolved polytomy (corresponding to the clade Eucrocopoda defined by Ezcurra [2016]) with *E. capensis*, *Proterochampsia* (sensu Ezcurra, 2016), *Dongusuchus efremovi* + *Yarasuchus deccanensis* (both of which have recently been reinterpreted as basal avemetatarsalians; Nesbitt et al., 2017), Phytosauria, and crown-group Archosauria. This node has a Bremer support of 3. Synapomorphies for this polytomy are (221, 1 to 0) exoccipital, medial margin of distal end: no contact with its counterpart; (227, 1 to 0) basioccipital-parabasisphenoid, basal tubera shape: clearly separated from each other; and (251, 1 to 0) prootic-parabasisphenoid, orientation of external foramina for N. abducens (CN VI): open anteriorly (character state unknown in *P. adorfi*).

A second set of analyses was conducted using MrBayes 3.2.6 (Ronquist et al., 2012) on CYPRES with the Mkv + G model. Rate variation across characters was sampled from a gamma distribution, and the analyses used four independent runs with two chains each, relative burn-in of 0.2, sampling at every 1,000 generations, for a total of 10,000,000 generations. The resulting majority rule tree differs from the result of the parsimony analysis in positioning *P. adorfi* closer to Archosauria, but this placement is not well supported, with a posterior probability for the node of only 0.515 (Fig. S3).

PALEOBIOLOGICAL IMPLICATIONS OF THE DENTITION

The presence of obliquely aligned, rather large denticles on the carinae of the maxillary and dentary tooth crowns of *Polymorphodon adorfi* (Fig. 4) resembles the condition in non-sauropod sauropodomorph dinosaurs (such as *Plateosaurus trossingensis*, SMNS 13200) and represents the first record of this dental morphotype in a non-archosaurian archosauriform. This morphotype has long been interpreted as evidence of herbivory in basal sauropodomorph dinosaurs (Galton, 1985; Martinez and Alcober, 2009) based on its resemblance to the teeth of extant plant-eating iguanid lizards (Montanucci, 1968; Melstrom, 2017). Barrett (2000) cautioned that *Iguana iguana* (green iguana) and closely related extant lizards can feed on a wide range of food-stuffs in captivity and thus should be considered omnivores rather than herbivores. However, Rand et al. (1990) observed that the diet of *I. iguana* in the wild is almost entirely plant-based, mostly comprising leaves, and Iverson (1982) demonstrated that various lizards including iguanines almost exclusively subsist on a plant diet. The teeth of *P. adorfi* indicate a diet different from those of contemporary archosauriforms and possibly omnivory.

Other non-archosaurian archosauriforms include Erythrosuchidae, which comprises the first macropredators among terrestrial reptiles during the Early and Middle Triassic (Gower, 2003; Butler et al., 2019), and several Middle to Late Triassic taxa such as Proterochampsidae (Trotteyn et al., 2013) and Doswelliidae (e.g., Schoch and Sues, 2014). Based on their dentitions, representatives of the latter two clades were carnivores, and at least some of them may have had a semiaquatic mode of life.

The two other archosauriform taxa reported to date from the Vellberg locality have teeth that indicate carnivorous habits. The doswelliid archosauriform *Jaxtasuchus salomoni* has slender, conical tooth crowns that bear apicobasal striations and resemble teeth of presumably piscivorous reptiles (Schoch and Sues, 2014; Schoch et al., 2018). The basal loricate *Batrachotomus kupferzellensis* has craniodental features, especially tall, labiolingually flattened, and recurved tooth crowns with serrated carinae, that establish it as a terrestrial apex predator in this tetrapod community (Gower, 1999). Clearly identifiable tooth marks left by this pseudosuchian on limb bones of the giant temnospondyl *Mastodonsaurus giganteus* provide direct evidence for this ecological role (Schoch et al., 2018).

There are several morphotypes of isolated teeth of archosauriform reptiles from the Upper Triassic Chinle Formation of the American Southwest (Heckert, 2004) that resemble the maxillary and dentary teeth of *P. adorfi*. One tooth taxon in particular, *Protecovasaurus lucasi*, is characterized by the presence of particularly large denticles that are obliquely inclined relative to the carinae (Heckert, 2004). Although superficially resembling those of early sauropodomorph or ornithischian dinosaurs and thus initially assigned to these groups, most of these tooth types cannot be assigned to any archosaurian clade at present due to the absence of associated non-dental remains. It is conceivable that some of them will eventually prove referable to non-archosaurian archosauriforms.

CONCLUSIONS

Polymorphodon adorfi is a new taxon of a non-archosaurian archosauriform reptile from the late Middle Triassic (Ladinian) of southern Germany. It is particularly distinguished by its heterodont dentition comprising conical premaxillary teeth and labiolingually flattened maxillary and dentary teeth, with both carinae bearing rather large serrations (denticles) that are

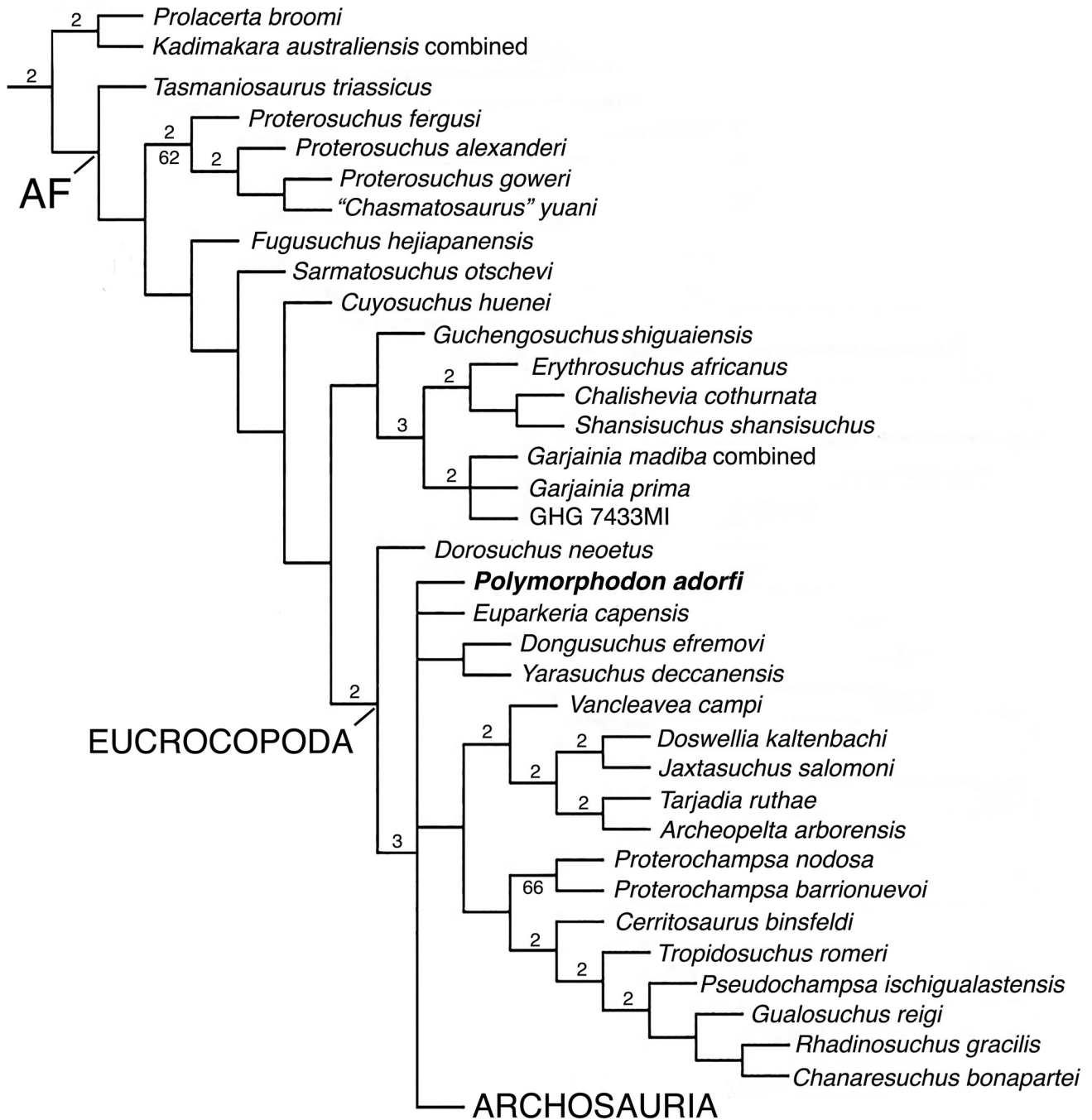


FIGURE 9. Strict consensus of eight trees recovered by parsimony analysis of the character-taxon matrix by Ezcurra (2016) with the addition of character states for *Polymorphodon adorfi* (in bold) using TNT 1.1. See text for additional details. The numbers above branches leading to nodes represent Bremer support values greater than 1, and the numbers below branches are bootstrap support values greater than 50%. The interrelationships among Archosauria (which includes Phytosauria in Ezcurra, 2016) are not detailed for layout reasons. **AF** denotes the clade Archosauriformes. **GHG 7433MI** has entered the literature in lieu of a species name.

obliquely aligned to the apicobasal axis of the tooth crowns. This tooth morphotype indicates a diet different from those of other non-archosaurian archosauriforms and possibly suggests omnivory. *Polymorphodon adorfi* further increases the known diversity of basal archosauriforms in terms of body plans and inferred modes of life.

ACKNOWLEDGMENTS

We are greatly indebted to the avocational collectors who donated important specimens from the Schumann quarry to the SMNS and provided much technical help during the museum's field campaigns: W. Kugler, F. Ullmann, B. Rozynek, P. Haubold, U. Günter, A. Bartholomä, and C. Straub. We thank the Schumann family for granting access to the site and for their continued generous support. N. Adorf, I. Rosin, M. Kamenz, and M. Battenstein

(all SMNS) participated in the excavations at the Schumann quarry. I. Rosin (SMNS) prepared the specimens with her customary skill. J. Rieger (Zeiss Metrology Services) undertook the micro-CT scanning of SMNS 91343. Free access to the TNT software is provided courtesy of the Willi Hennig Society. H.-D.S. gratefully acknowledges receipt of an Alexander von Humboldt Award for Excellence in Research and Teaching. We thank J. B. Desojo, H. Hagdorn, S. L. Nesbitt, and D. Seegis for discussions. G. Bever, C. Foth, and an anonymous reviewer offered helpful comments on a draft of the manuscript.

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