

**THE MARINE PACHYPLEUROSAUR *SERPIANOSAURUS GERMANICUS* NOV. SPEC. –
SKELETON AND ISOLATED BONE REMAINS FROM THE PELSONIAN
(MIDDLE TRIASSIC) OF THE EUROPEAN GERMANIC BASIN
CARBONATE INTERTIDALS AND ITS PALEOBIOLOGY AND TAPHONOMY**

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Abstract—The large marine pachypleurosaur sauropterygian *Serpianosaurus germanicus* nov. spec., representing the oldest well known record of this genus from the Pelsonian, is introduced based on a postcranial skeleton. Of younger age are the *Serpianosaurus mirigolensis* (Rieppel, 1989) specimens from the Illyrian/Fassanian boundary (Grenzbitumen Bed) of the northwestern Tethys (Monte San Giorgio). Additional materials from Germany contain individual remains of different sexes and ages, all of which have been found in shallow marine to intertidal carbonate deposits. The postcranial skeleton and single bone remains from the Karlstadt Formation (upper Pelsonian, Anisian) of the Middle Triassic from different German sites demonstrate that this genus is more common in the Germanic Basin, but also is present in the northern Tethys. The paleogeography and facies distribution indicate evaporative to shallow marine conditions with extensive intertidal flats and sabkhas on the southern Germanic Basin coasts at that time. One possible reason for the abundance of *Serpianosaurus* during late Pelsonian time is a food chain that was based on horseshoe crabs, the eggs of which might have been a main target for the fish that were the primary food source for the pachypleurosaurs. *Serpianosaurus* and other marine vertebrates may have been killed by storm events and their carcasses deposited on intertidal flats where they were themselves food sources for large carnivorous thecodont archosaurs such as *Ticinosuchus* (*Chirotherium* tracks), or *?Arizonasaurus* (*Isochirotherium* tracks), the footprints of which occur on the intertidals where *Serpianosaurus* and other marine vertebrate remains were deposited.

INTRODUCTION

Isolated humeri from the Middle Triassic Lower Muschelkalk Schaumkalk beds of Jena (Middle Germany, Central Europe) were first attributed to “*Nothosaurus*” by Meyer (1847-1855), and later to “*Phygosaurus*” by Arthaber (1924), whereas a new description of a humerus from Freyburg a. d. U. was attributed to “*Cymatosaurus*” (Rieppel and Wernburg, 1998), a genus for which the postcranial skeleton has not yet been described.

The herein described skeleton from Central Germany (Fig. 1) was initially attributed to “*Serpianosaurus*” (Diedrich and Trostheide, 2007). Further discussions of the skeletal and isolated bone material from Germany are lacking, but historical finds including postcranial skeleton remains, and new isolated bone discoveries are described herein. Also presented are the taphonomy and paleoecological background, and the bio- and chronostratigraphy based on track bed correlations in the Germanic Basin (Diedrich, 2008). Additionally, new excavations in the carbonates of the intertidal mud flats of the Germanic Basin provide a complete picture of the habitat of the carbonate tidal flats, the terrestrial reptile biodiversity as represented by trackways, and abundant horseshoe crab traces potentially recording seasonal migrations and reproduction in the beach zone (Diedrich, 2009). There, new bone material of *Serpianosaurus* has been discovered together with other marine reptile and fish remains (Diedrich, 2009).

The aim of this paper is the description of a new *Serpianosaurus* species that appears in younger strata. This is compared with the well-known complete skeleton of *Serpianosaurus mirigolensis* (Rieppel, 1989). The paleoenvironment in which these fossils occur is examined through the discussion of invertebrate tracks (*Koupichnium*, attributed to horseshoe crabs), and other vertebrate remains (fish, sharks and other marine reptiles).

GEOLOGY AND SEDIMENTOLOGY

The strata of the Lower Muschelkalk of the Middle Triassic in Central Germany consist of about 110 m of carbonates. These include

the older Jena Formation (cf. Bachmann et al., 2008) and the younger Karlstadt Formation of the basal Middle Muschelkalk (Diedrich, 2012; Fig. 2). The Aegean to Pelsonian aged Jena Formation carbonates are approximately 90 m thick and consist of shallow marine deposits, mainly “Wellenkalk” and shell- or ooid-rich limestones (Knaust, 2000; Bachmann et al., 2008; Diedrich, 2012). At Bernburg, the Jena Formation consists of debris flows, mass flows and intraclast conglomerates, or slickensided beds with sinusoidally deformed veins (Diedrich, 2012). These are typical of seismic-influenced sediments in shallow sub-tidal zones (cf. Kurze, 1981; Knaust, 2000; Föhlisch and Voigt, 2001; Bachmann and Aref, 2005; Diedrich, 2009, 2012). The positions of seismic epicenters in the Jena Formation have previously been inferred from studies on slickensided orientations in the shallow submarine carbonates (Föhlisch, 2007; Diedrich, 2012).

At Bernburg three major bone bed layers are present in the muS or Schaumkalk substage, which also contains the *Serpianosaurus* remains figured herein. The marine sauropterygian reptile (no terrestrial reptiles) and fish remains (mainly scales) are found in Bernburg with a monospecific fauna consisting of the abundant, small, hypersaline-adapted bivalve *Neoschizodus orbicularis*, concentrated in shallow sub-tidal channels (Diedrich, 2009, 2012) under conditions similar to those described for the southern German site Eberstadt (Hagdorn and Simon, 1993). Similar in age is the shallow marine oolite facies of the Schaumkalk substage of the upper Jena Formation in Jena, where *Serpianosaurus* bones were also collected historically.

The Karlstadt Formation (or mm1) carbonates within the *Judicarites zoldianus* cephalopod biozone at the top of the Pelsonian (middle Anisian) contain the articulated *Serpianosaurus* skeletons described herein and isolated bone remains only in the intertidal facies. These can be correlated throughout the Germanic Basin with a megatracksite in the northern Tethys (Diedrich, 2008, 2012). The Karlstadt Formation carbonate sediments comprise 5.15 meters of lagoon platy dolomitic limestones, 2.5 meters of variable mud-cracked biolaminated and thin, micritic to arenitic, carbonates (Diedrich, 2009, 2011, 2012; Fig. 2). The chrono-, bio- and lithostratigraphic data and the

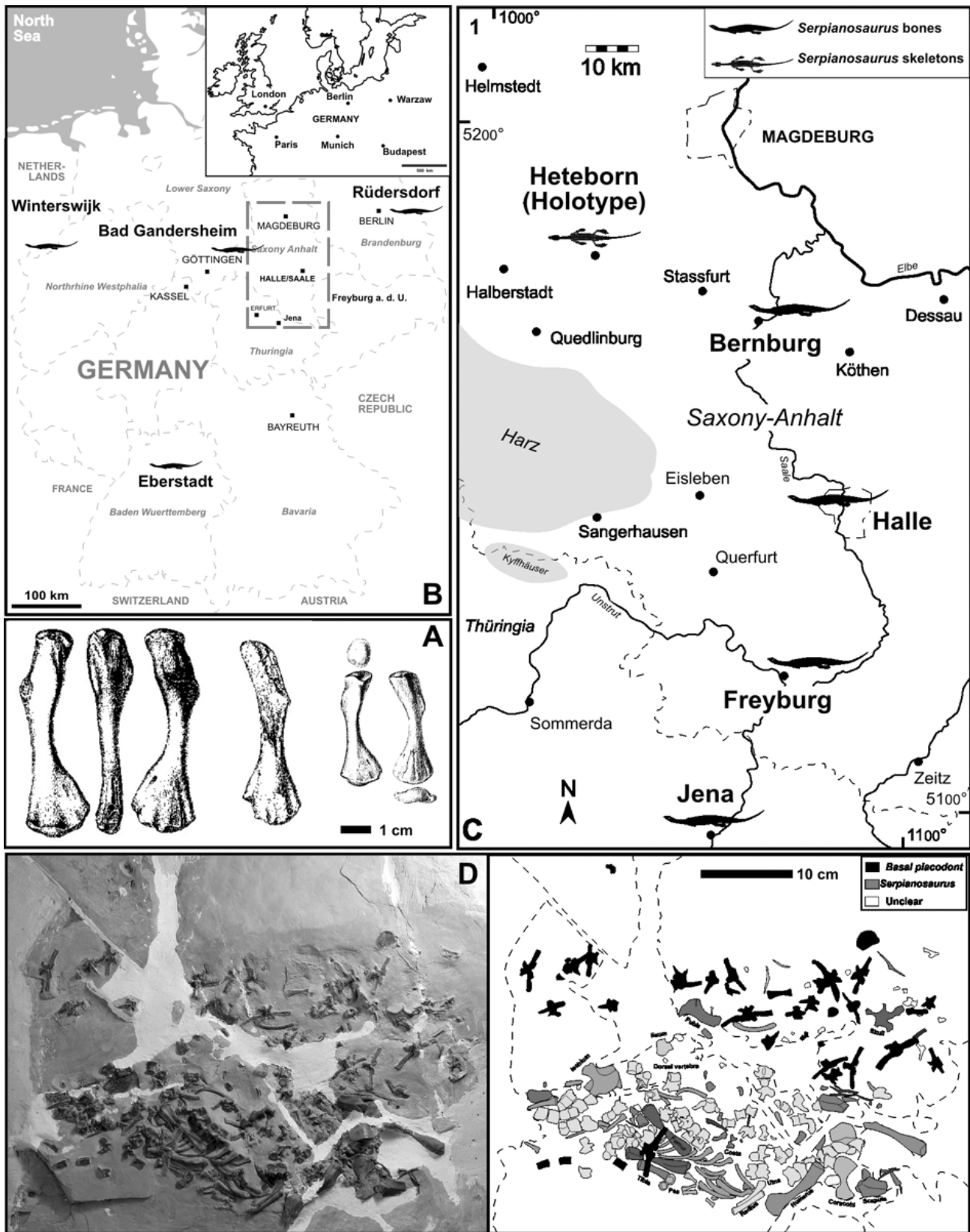


FIGURE 1. A, *Serpianosaurus* humeri figured from the Schaumkalk or Saurierkalk at the top of the Jena Formation, (Pelsonian, Anisian) of Jena (from Meyer 1847-1855). B-C, Sauropterygian large pachypleurosaur *Serpianosaurus germanicus* nov. spec. localities in Middle Germany in “Lower/Middle Muschelkalk” limestone quarries of Pelsonian age (Anisian, Middle Triassic). D, Basal placodont (*Paraplacodus* or *Saurosphargis*) postcranial skeleton remains consisting mainly of a dorsal vertebral column and a few forelimb and pectoral girdle bones from the Bithynian, mixed with another marine large pachypleurosaur *Serpianosaurus* sp. skeleton found on intertidal biolaminates at Winterswijk, Netherlands in the western Germanic Basin (cast in the ME no. Wi-1, original in the NL no. NMNHL RGM 449487).

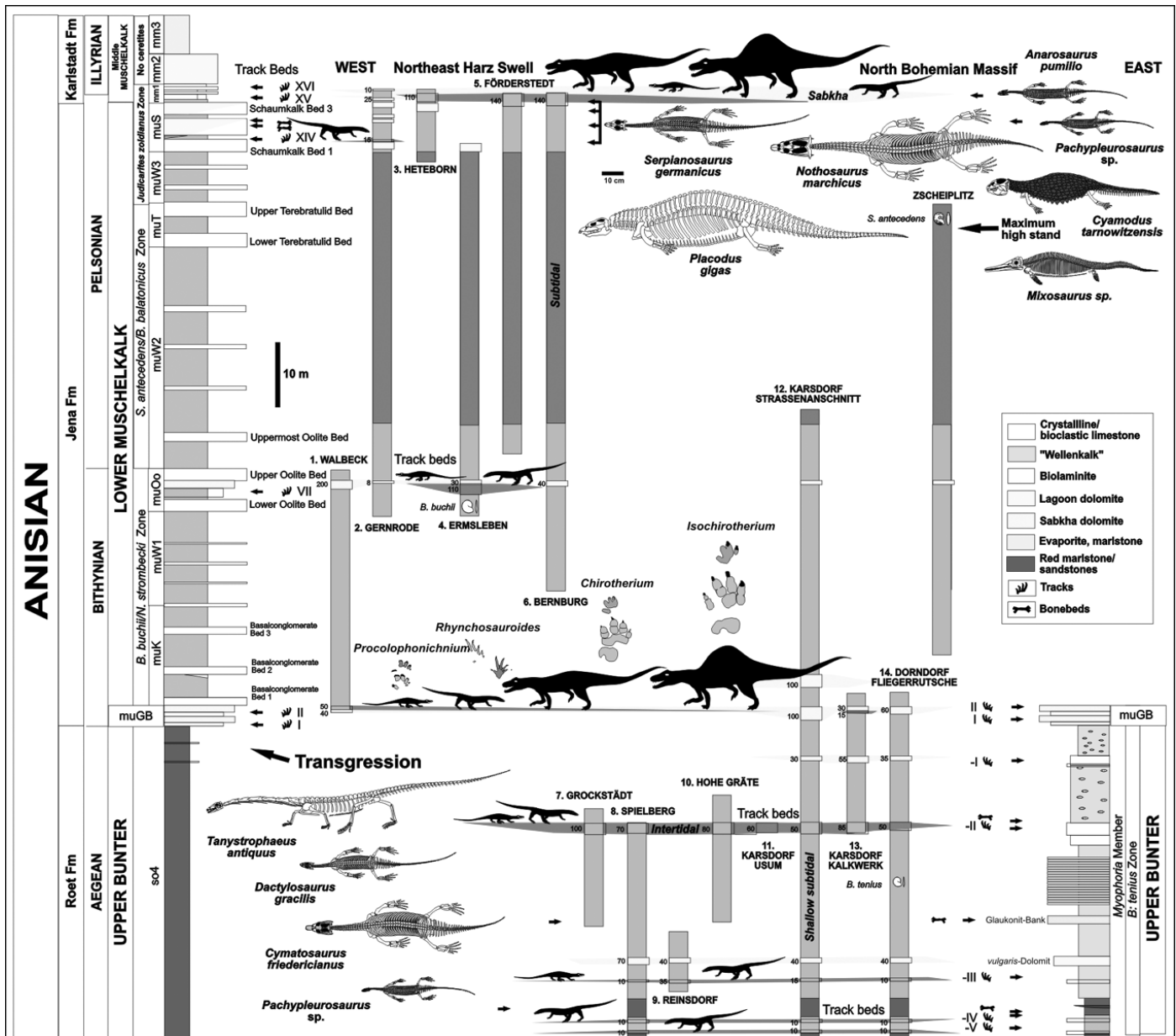


FIGURE 2. *Serpianosaurus* and marine reptile and terrestrial reptile track remains in Central Germany in the Upper Bunter to Lower Muschelkalk (modified after Diedrich and Trostheide, 2007).

ichnostratigraphy were additionally dated through the correlation of ceratite zones (Diedrich, 2008, 2012). In both Heteborn and Förderstedt the Karlstadt Formation has similarly developed platy limestone to intertidal facies as at Bernburg. The *Serpianosaurus germanicus* nov. spec. holotype skeleton attached slab is a 3 cm thin micrite, which has negatives of under- and overlying biolaminar mud cracks. The Karlstadt Formation seems to represent a Milankovitch cycle (about 400,000 years in carbonate cycles/sequences: Aigner and Bachmann, 1992).

MATERIAL AND METHODS

In the historical collections of the Naturkundemuseum Magdeburg (= NMM) and the Martin-Luther Universität Halle/Saale (= MLU.IGF) postcranial skeleton remains of Heteborn and Förderstedt and some isolated bones from Jena and Freyburg a. d. U. were used for this analysis of large pachypleurosaurs from the Pelsonian Middle Triassic carbonates of Middle Germany. The material from Eberstadt was studied in the Muschelkalkmuseum Ingelfingen (= MMI). Some material of Bad Gandersheim is housed in the Museum of Natural History of the Humboldt

University Berlin (= MB). New excavations in the Pelsonian-aged carbonates resulted in additional isolated bone material from the Bernburg locality, which was identified with the postcranial skeleton remains being housed in the Landesmuseum für Ur- und Frühgeschichte Sachsen-Anhalt in Halle/Saale (= LDA).

PALEONTOLOGY

Reptilia Laurenti, 1768

Superorder Sauropterygia Owen, 1860

Order Nothosauroida Baur, 1889

Suborder Pachypleurosauria Nopcsa, 1928

Family Pachypleurosauridae Nopcsa, 1928

Genus *Serpianosaurus* Rieppel, 1989

Serpianosaurus germanicus nov. spec.

Figs. 3-4

Type species: *S. mirigiolensis* Rieppel, 1989 from the

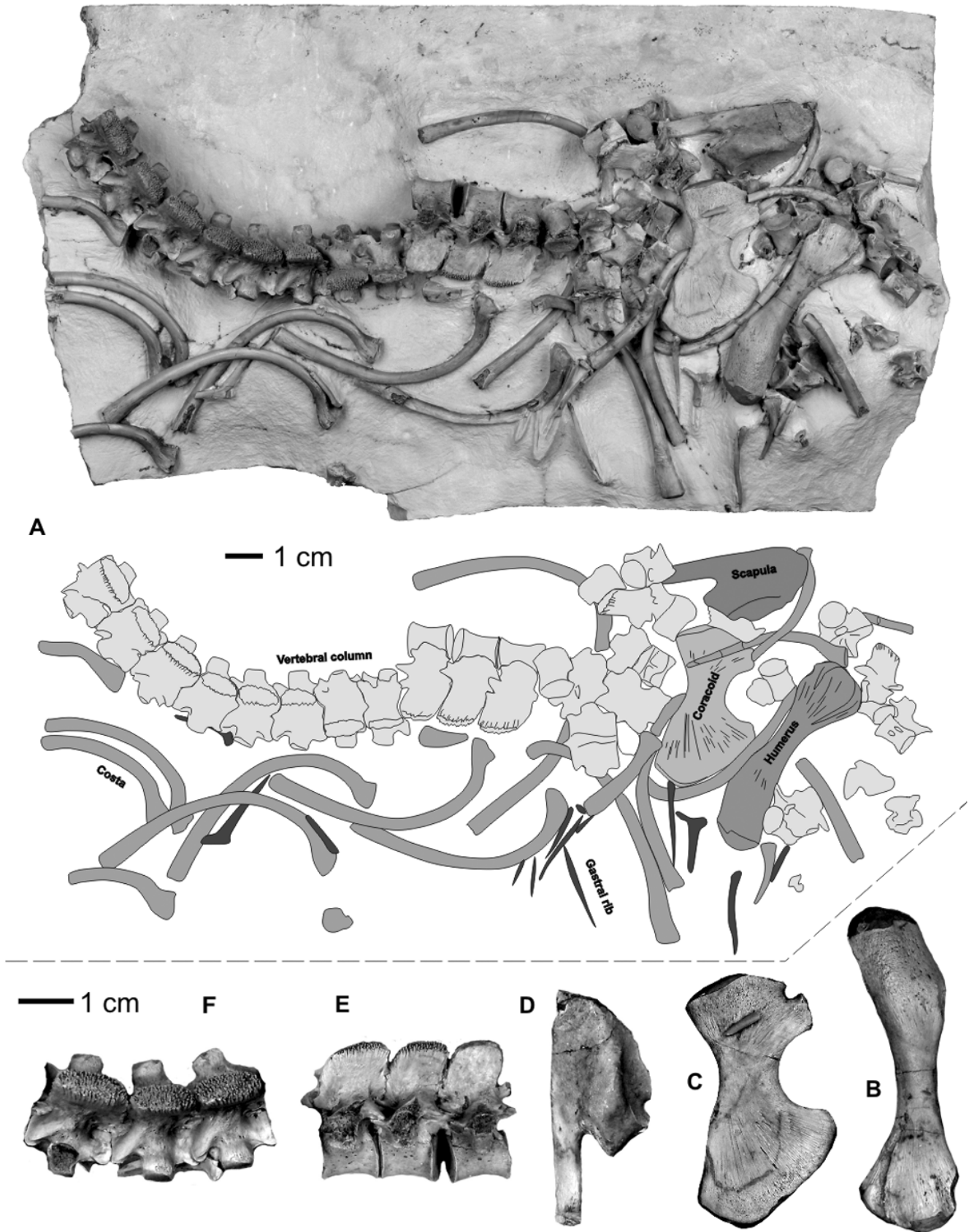


FIGURE 3. A, *Serpianosaurus germanicus* nov. spec. postcranial holotype skeleton (NMM no. 2329) from the Karlstadt Formation, latest Pelsonian (Middle Anisian, Middle Triassic) of Heteborn (Saxony-Anhalt, Middle Germany). B, Humerus, ventral view. C, Coracoid, ventral view. D, Scapula, ventral view. E, Middle thoracic vertebrae, lateral view. F, Posterior thoracic vertebrae, dorsal view.

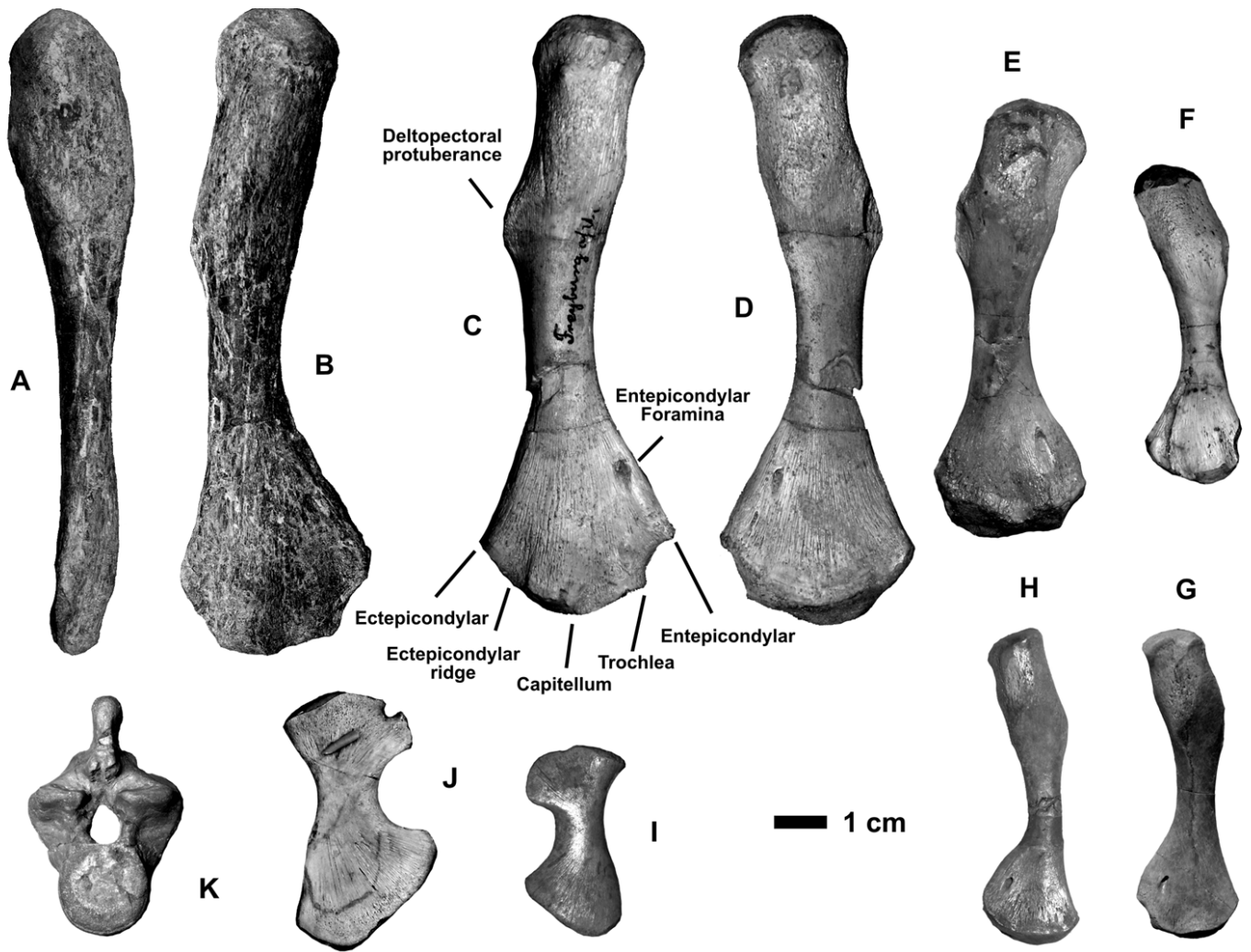


FIGURE 4. *Serpianosaurus germanicus* nov. spec. humeri from Middle Germany of the Jena Fm and the Karlstadt Fm, Pelsonian (Anisian, Middle Triassic). **A-B**, Humerus of a fully grown up animal found in an *Isochirotherium* trackway in the intertidal seismic shocked biolaminates of the Upper Pelsonian at Bernburg (coll. MLUFG without no., see also Fig. 5), **A**, lateral inner side, **B**, ventral. **C-D**, Humerus of a fully grown up animal found in the Upper Pelsonian of Freyburg a. d. U. (“*Cymatosaurus*” original in Rieppel, 1995), **C**, ventral, **D**, dorsal. **E**, Humerus of a younger individual from Bad Gandersheim (coll. MB no. R16). **F**, Humerus of a younger individual of the skeleton of Heteborn (NMM no. 2329), dorsal. **G**, Humerus of a younger individual from Eberstadt (MMI no. 1193/2), dorsal. **H**, Humerus of a younger individual from Eberstadt (MMI no. 1193/57), dorsal. **I**, Coracoid of a very young individual found in the Upper Pelsonian of Freyburg a. d. U. (NMB without no.), ventral. **J**, Coracoid of a younger individual of the skeleton of Heteborn (NMM no. 2329), ventral. **K**, Dorsal vertebra found in the Upper Pelsonian of Freyburg a. d. U. (NMB without no.), cranial.

Grenzbitumen Bed, Illyrian/Fassanian boundary, Anisian/Ladinian boundary, Middle Triassic of Monte San Giorgio, Tessin, Switzerland (Fig. 5).

Holotype: Postcranial skeleton including the dorsal vertebral column, dorsal and gastral ribs, one scapula, one coracoid and one humerus (NMM no. 2329).

Type locality: Historical limestone quarry at Heteborn, Saxony-Anhalt, Middle Germany, Central Europe.

Type stratum: 3 cm thick tempestite/tsunamiite layer intercalated into the biolaminates of the Karlstadt Fm (= mm1 Substage), basal Middle Muschelkalk, latest Pelsonian, Middle Anisian, Middle Triassic.

Differential diagnosis: The shapes of pectoral and forelimb bones (Figs. 4.1-6, 6) are different from those of the similar-sized *Serpianosaurus mirigiolensis*, the described skeletons of which were not complete in several cases, as a result of bone overlap or tectonic deformation (cf. Rieppel, 1989).

The scapula of the new species is less diagnostic and is similar to the described one of *Serpianosaurus mirigiolensis* (cf. Rieppel, 1989). In contrast, similar-aged *Nothosaurus marchicus* scapulae, which are of the same size, have an interiorly convex lateral outer margin (cf. *N. marchicus* skeleton and bones in Arthaber, 1924). *Serpianosaurus* has a straight lateral margin.

A complete coracoid allows a good comparison to isolated ones from the Pelsonian marine deposits of Central Germany (Figs. 4.7-8). Both coracoids of *Serpianosaurus mirigiolensis* have not been completely illustrated (Rieppel, 1989). Nevertheless, the shape of the coracoid of *S. mirigiolensis* differs from the new species. The inner lateral margin of the coracoid of the new species is nearly full, half-round and concave, which is more oval in *S. mirigiolensis*. Those young individuals of *S. germanicus* (Figs. 4.7-8) already have this characteristic, but the foramen seems better developed in older individuals (Fig. 4.6). In similar-aged *Nothosaurus marchicus* the coracoids are much more elongated with a very different general shape (cf. Arthaber, 1924).

Humeri of similar shape from different localities (Figs. 1 and 4.1-6) and most probably of different aged and sexed individuals, all from the upper Jena Formation and Karlstadt Formation (Pelsonian) of Middle Germany, are more similar to those of *S. mirigiolensis* (Rieppel, 1989), because distally they are wider and longer, especially in the older individuals.

The dorsal vertebrae of *Serpianosaurus mirigiolensis* and *S. germanicus* are similar to each other. Their shape is different from *Nothosaurus marchicus* of similar age. The end of the dorsal spines in *Serpianosaurus* is thickened and finally flattened with a unique granular surface (Figs. 3E-F, 4.9), being typical only for this genus (cf. Rieppel, 1989).

DISCUSSION

Biostratigraphy and Paleobiogeography

In Europe the oldest record of *Serpianosaurus* sp. from the basal Lower Muschelkalk of Winterswijk (Bithynian; Fig. 7) was incorrectly described as "*Cymatosaurus* sp." (Oosterink et al., 2003) as single humeri were attributed to this genus by Rieppel (2000) and Oosterink et al. (2003). Meyer (1847-1855) illustrated two humeri from the upper Lower Muschelkalk ("Saurierkalk or Schaumkalk"), which consists of massive oolite beds in the Jena Formation (Pelsonian, Lower Anisian, Figs. 1-2). This material, and the herein newly described skeleton and isolated bone material, is intermediate in age between the Winterswijk (Bithynian) and the Monte San Giorgio (Fassanian) and Perledo (Longobardian) specimens of *Serpianosaurus* (cf. Rieppel, 1989; Fig. 7). Also, bone material from the Karlstadt Formation of Eberstadt in southern Germany seems to have been incorrectly attributed to "*Anarosaurus*" (Hagdorn and Simon, 1993), whereas two humeri described herein (Figs. 4.5-6) are at least similar to those of smaller individuals of *Serpianosaurus*. *Anarosaurus* has smaller, less distally widened and more slender humeri (see re-figured *Anarosaurus* holotype skeleton and humerus in Diedrich and Trostheide,

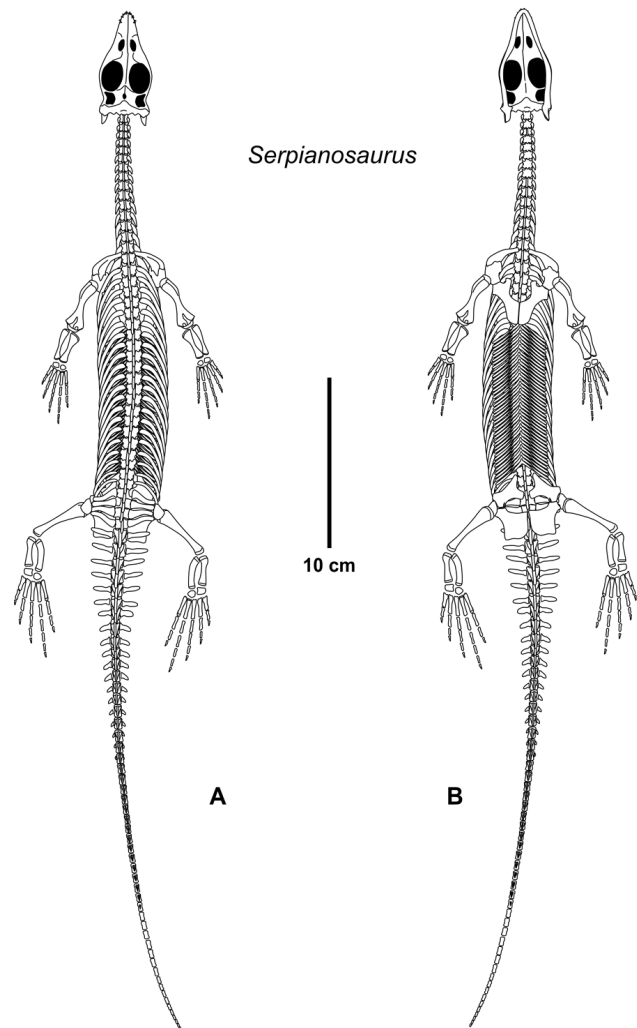


FIGURE 5. Skeletal reconstruction of *Serpianosaurus mirigiolensis* in **A**, dorsal and **B**, ventral views. Based on the holotype described by Rieppel (1989).

2007). Both *Anarosaurus* and *Serpianosaurus* are present in the Karlstadt Formation (latest Pelsonian) across the Germanic Basin, but have not been well separated in isolated bone material in the past. Here a new species can be reported with *S. germanicus* nov. spec. from the upper Lower Muschelkalk and lower Middle Muschelkalk (all Pelsonian in age) of Heteborn and other sites in Middle Germany. This species is not synonymous with the younger aged Italian Besano finds of *Serpianosaurus zinae*, which seem to be the youngest record of this genus (Fig. 7). The older "Lower Muschelkalk" *S. germanicus* n. sp. species (Bithynian/Pelsonian) is stratigraphically followed by an "Upper Muschelkalk" (Illyrian/Fassanian) species, *Serpianosaurus mirigiolensis* from the Swiss Monte San Giorgio lagoons (Rieppel, 1989; Fig. 7). Further, a younger-aged species was thought to have been recorded from the latest Lower Keuper (Longobardian) with "*Phygosaurus perledicus*" Arthaber, 1924 of the Italian Perledo lagoons (Deecke, 1886; Peyer, 1934), but this was declared a *nomen nudum* and to be a different pachypleurosaur, of which the holotype material is lost in Strassbourg (Rieppel, 1989).

Taphonomy, Paleobiology and Habitat

Serpianosaurus remains are recorded with single bones from the oolitic bar facies of the Lower Muschelkalk in the Germanic Basin, which was deposited between 1-3 meters water depth (Knaust, 2000).

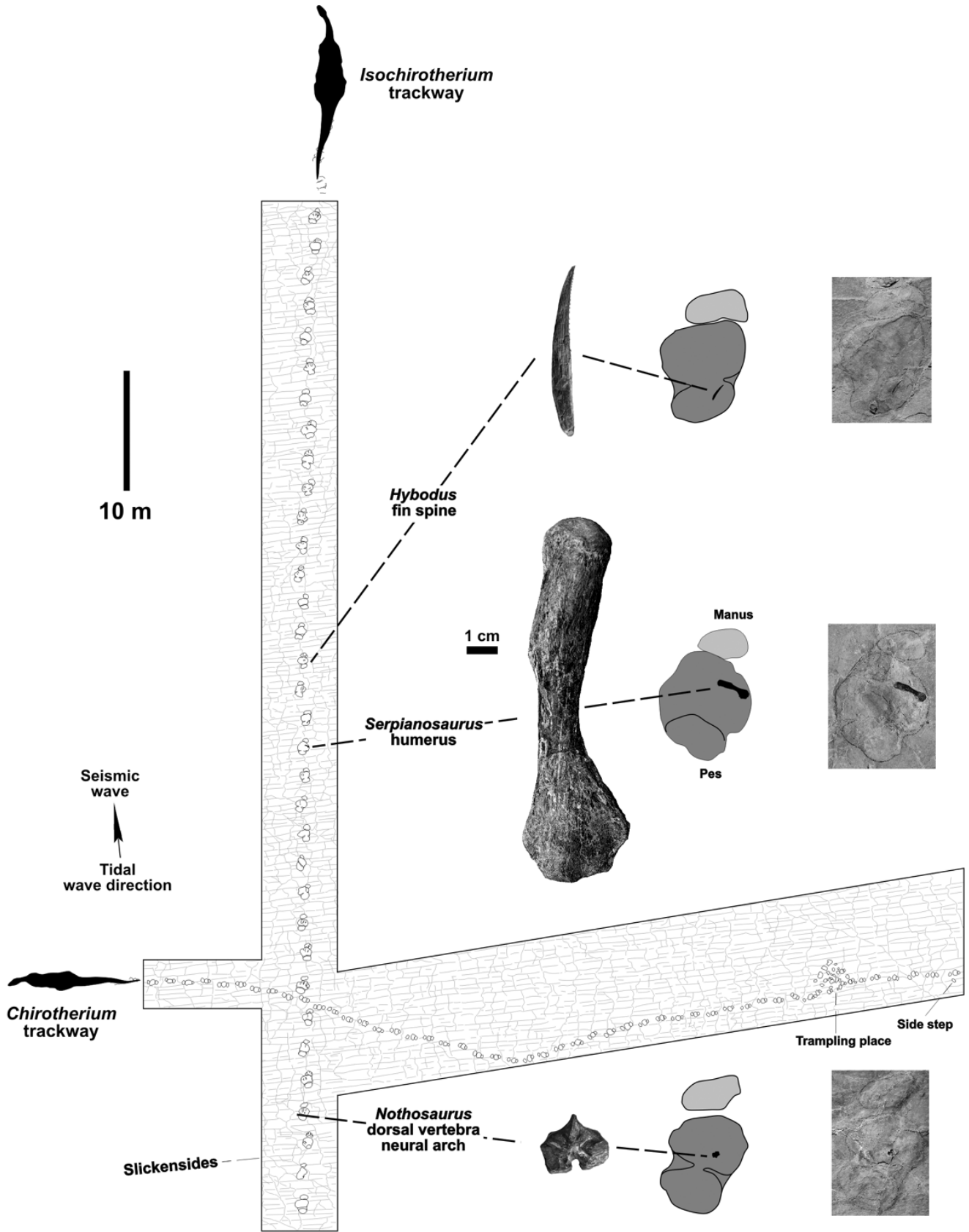


FIGURE 6. Taphonomy of *Serpianosaurus germanicus* nov. spec. A humerus was washed into a large *Isochirotherium herculis* trackway, along with bones of *Nothosaurus marchicus* and *Hybodius* sp. shark fin spine remains. This giant archosaur trackway was crossed by a *Chirotherium barthi* trackway on seismic (tsunamiites) carbonate intertidal biolaminates in the Karlstadt Formation (latest Pelsonian) of Bernburg (Middle Germany, modified from Diedrich, 2009).

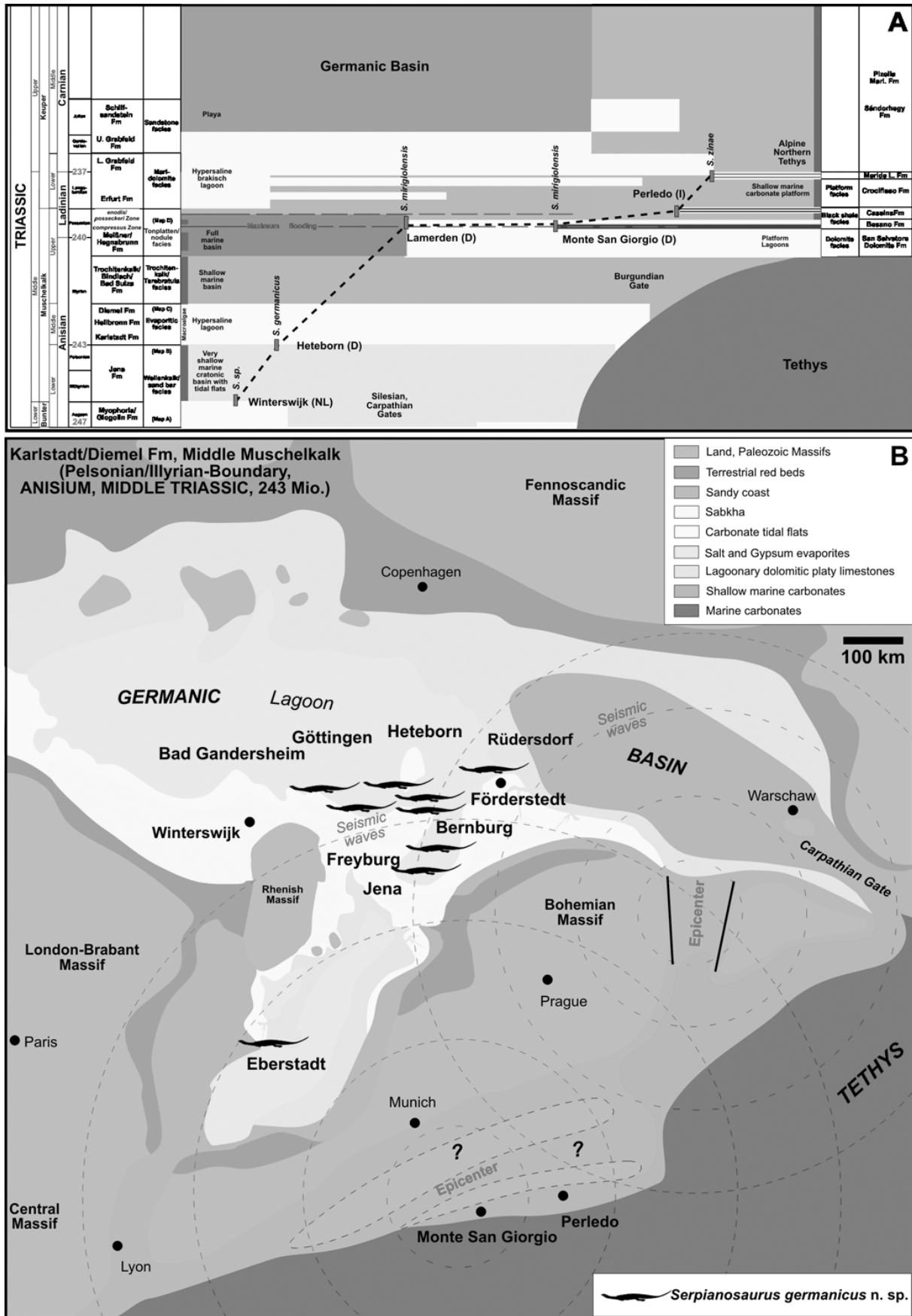


FIGURE 7. Paleobiogeography of *Serpianosaurus germanicus* nov. spec. in lagoons of the shallow marine Germanic Basin with extended low relief intertidal coasts during the Pelsonian/Illyrian boundary (paleogeography after Diedrich, 2008).

The platy limestones of the Karlstadt Formation, instead, are lagoon to intertidal deposits (Diedrich, 2012). Only in these biolaminated series at the German Heteborn site, similar to the biolaminates at the Dutch site Winterswijk (Oosterink et al., 2003), are articulated skeletons of different marine reptiles preserved. Track-maker skeletons, however, are “absent.” The best explanation of this taphonomic phenomenon in this unique intertidal flat setting is the action of tsunami or storm events, during which living marine animals were transported up to tens of kilometers onto the carbonate mud flats (Diedrich, 2009). The low relief (only about 50 cm relief) of the mud flats surrounding the Germanic Basin coasts (Diedrich, 2008; Fig. 7) did not allow marine animals, which may have survived such events, to move back to the ocean as paraxial swimmers. Other animals were possibly killed during those quick floods, where sediments of tempestites/tsunamites (= arenite layers in biolaminates) covered the carcasses quickly. Furthermore, daily tides dislocated most of the skeletons, although single bones were trapped in the depressions of large chirotherid tracks (Diedrich, 2009; Fig. 6), and were mainly washed into the lagoonal tidal channels (as accumulations with *Neoschizodus* shells) and oolite bars, where they built up “bonebed layers.” Conversely, bones are fully absent in the deeper marine areas (= Wellankalk facies) of the shallow Germanic Basin. Similar *Serpianosaurus* finds are from the northwestern Tethys (Monte San Giorgio, Perledo), but those were found in subtidal black shale deposits of Prealpine lagoons (Furrer, 1995, 2003; Rieppel, 1989). Mortality during reproduction for *Serpianosaurus* can be excluded because it is well-known that pachypleurosaurs and other sauropterygians gave live birth in the water, and did not deposit eggs in nests on the coastal sandy beaches (Cheng et al., 2004).

Serpianosaurus germanicus nov. spec. likely was a fish hunter in the lagoons, based on its spiky dentition, which has similar anterior large fang teeth and small teeth in the posterior, as in *Nothosaurus mirabilis* (cf. Arthaber, 1924; Rieppel, 2000). The *Serpianosaurus* humerus from the Berburg site is important for understanding its position in the food chain (Fig. 8). The intertidals of the Lower/Middle Muschelkalk and especially at the time of the Karlstadt Formation (uppermost Pelsonian) were mud flats that were sites of reproduction for horseshoe crab populations, which apparently migrated seasonally with ten thousands of individuals into the Germanic Basin (Diedrich, 2011). Millions of horseshoe crab eggs would have formed the base of a food chain. Fish, which are abundant in the Middle Muschelkalk lagoons with species such as *Gyrolepis*, *Colobodus*, *Saurichthys* and most commonly *Eosemionotus vogeli* Fritsch, 1906 (Schultze et al., 1986), which occur also in the basal Middle Muschelkalk layers (Karlstadt Formation) of Förderstedt and other northern to middle German sites (Stolley 1920, Schultze et al., 1986), might have fed mainly on these eggs. Those fish, living in schools, were themselves hunted by different sauropterygians, such as *S. germanicus* and *Nothosaurus marchicus*, and even by sharks such as *Hybodus* (see Diedrich, 2009). Carcasses of these were consumed by large-sized carnivorous thecodont archosaurs such as *Ticinosuchus* (*Chirotherium* trackways) or *Arizonasaurus* (*?Isochirotherium* trackways) (Fig. 8B), in addition to smaller archosauromorphs, evidenced by *Macrocnemus* trackways (*Rhynchosauroides* track type) (Diedrich, 2009). The thecodont archosaurs may have migrated long distances over the Pangea globe specifically for this “limulid reproduction event” when food was ample on the extensive intertidals and coasts of the Germanic Basin (Diedrich, 2011, 2012).

CONCLUSION

The large pachypleurosaurs sauropterygian *Serpianosaurus* is known from the Bithynian in Europe and existed up to the Longobardian,

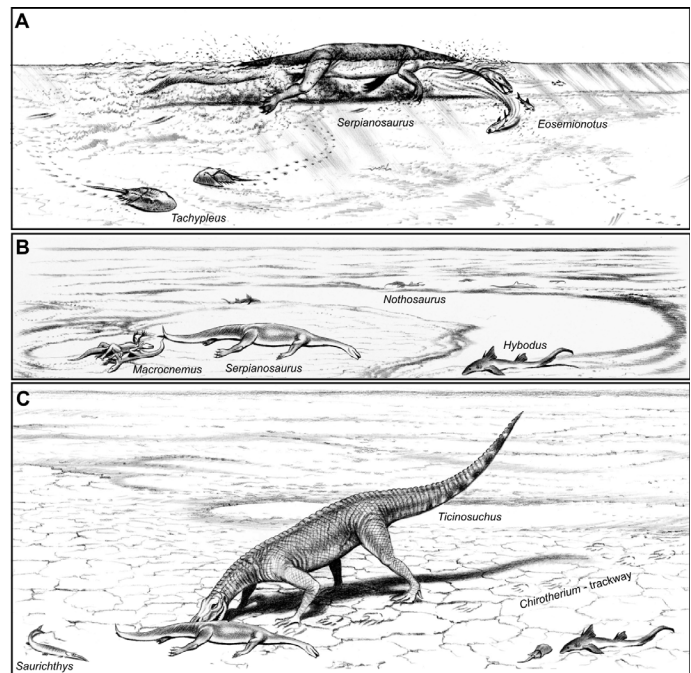


FIGURE 8. Intertidal carbonate mush flats on the margins during the Upper Pelsonian of the Germanic Basin (Central Europe) and its reptile food chain. **A**, *Serpianosaurus germanicus* nov. spec. hunting within the flood tide for actinopterygian fish such as common *Eosemionotus* (which fed on horse shoe crab eggs); on the intertidal biolaminates under shallow water conditions horseshoe crabs reproduced in large populations. **B**, Marine and terrestrial reptiles and fish killed in a tsunami wave that flooded far onto the extensive intertidal flats. **C**, Feeding of the *Chirotherium* trackmaker, the thecodont archosaur *Ticinosuchus* on marine reptiles such as *Serpianosaurus* (modified from Diedrich, 2009, illustrations by G. Teichmann).

possibly with up to four different species that might represent a monophyletic line. All remains are restricted to lagoonal deposits in the Germanic Basin (The Netherlands, Germany) and the northwestern Tethys pre-alpine lagoons (Switzerland, northern Italy). In the Germanic Basin skeletal remains occur in intertidal biolaminates or tsunamite/tempestite layers. Single bones were found in large isochirotherid tracks of the intertidal zones, which were limulid reproduction zones across the southern Germanic Basin during the latest Pelsonian. *Serpianosaurus* was unable to survive severe storm or tsunami events if carried far onto the extensive carbonate intertidals. Here, the carcasses were partly scavenged by archosaurs, which fed also on horseshoe crabs during their mass reproduction seasons. The latter were an essential part of a food chain, as they were a food source for fish that ultimately fed different aquatic sauropterygian reptiles, such as *Serpianosaurus*.

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