

# A new basal sphenacodontid synapsid from the Late Carboniferous of the Saar-Nahe Basin, Germany

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Fröbisch, J., Schoch, R.R., Müller, J., Schindler, T., and Schweiss, D. 2011. A new basal sphenacodontid synapsid from the Late Carboniferous of the Saar-Nahe Basin, Germany. *Acta Palaeontologica Polonica* 56 (1): 113–120.

A new basal sphenacodontid synapsid, represented by an anterior portion of a mandible, demonstrates for the first time the presence of amniotes in the largest European Permo-Carboniferous basin, the Saar-Nahe Basin. The new taxon, *Cryptovenator hirschbergeri* gen. et sp. nov., is autapomorphic in the extreme shortness and robustness of the lower jaw, with moderate heterodonty, including the absence of a greatly reduced first tooth and only a slight caniniform development of the second and third teeth. *Cryptovenator* shares with *Dimetrodon*, *Sphenacodon*, and *Ctenospondylus*, but notably not with *Secodontosaurus*, enlarged canines and a characteristic teardrop outline of the marginal teeth in lateral view, possession of a deep symphyseal region, and a strongly concave dorsal margin of the dentary. The new find shows that sphenacodontids were present in the Saar-Nahe Basin by the latest Carboniferous, predating the record of sphenacodontid tracks from slightly younger sediments in this region.

Key words: Synapsida, Sphenacodontidae, Carboniferous, Saar-Nahe Basin, Germany.

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Received 21 April 2010, accepted 12 September 2010, available online 16 September 2010.

## Introduction

The Saar-Nahe Basin of southwest Germany is among the largest and best-studied of late Palaeozoic sedimentary basins, and has yielded the largest quantities of vertebrate fossils for that time interval in Europe (Boy 2007). Several thousand specimens of fishes and amphibians have been collected from numerous successive lake deposits at various localities in the last decades (Boy 1987; Schindler and Heidtke 2007; Schoch 2009). These often exquisitely preserved discoveries have provided profound insights into the palaeobiology of aquatic taxa, and the palaeoecology and taphonomy of these richly-documented faunas (Boy 2003). However, despite intensive search, not a single tetrapod other than the abundant aquatic amphibians was found in the more than 165 years of collecting in this basin. This differs from the record of other basins (Lodève, Autun, Thuringian Forest, Döhlen), which have all yielded a range of fully terrestrial taxa (Boy 1977; Werneburg and Schneider 2006).

The absence of amniote skeletons in the Saar-Nahe Basin is also in a stark contrast to the rich amniote track record reported from the same area (Haubold 1973; Fichter 1983; Voigt 2007). According to this evidence, diadectids, parareptiles, diapsids, and synapsids are likely to have been present in the Saar-Nahe Basin. One particularly obvious group of fully terrestrial tetrapods that diversified rapidly and that represents the dominant element in Late Palaeozoic terrestrial vertebrate ecosystems are synapsid amniotes, which ultimately led to the evolution of mammals (e.g., Olson 1966). The synapsid tracks of the Saar-Nahe Basin agree with skeletal finds from other, roughly coeval basins, such as Autun (Gaudry 1886; Currie 1979), Thuringian Forest (Berman et al. 2001, 2004), Döhlen in Saxony (Credner 1888; Huene 1925; Currie 1979), and Upper Silesia (Schroeder 1905).

Synapsids are traditionally divided into two major groups, the paraphyletic grade of “pelycosaurs” and the monophyletic Therapsida, which includes mammals (e.g., Romer and Price 1940; Kemp 1982, 2005; Reisz 1986). As “pelycosaurs” do

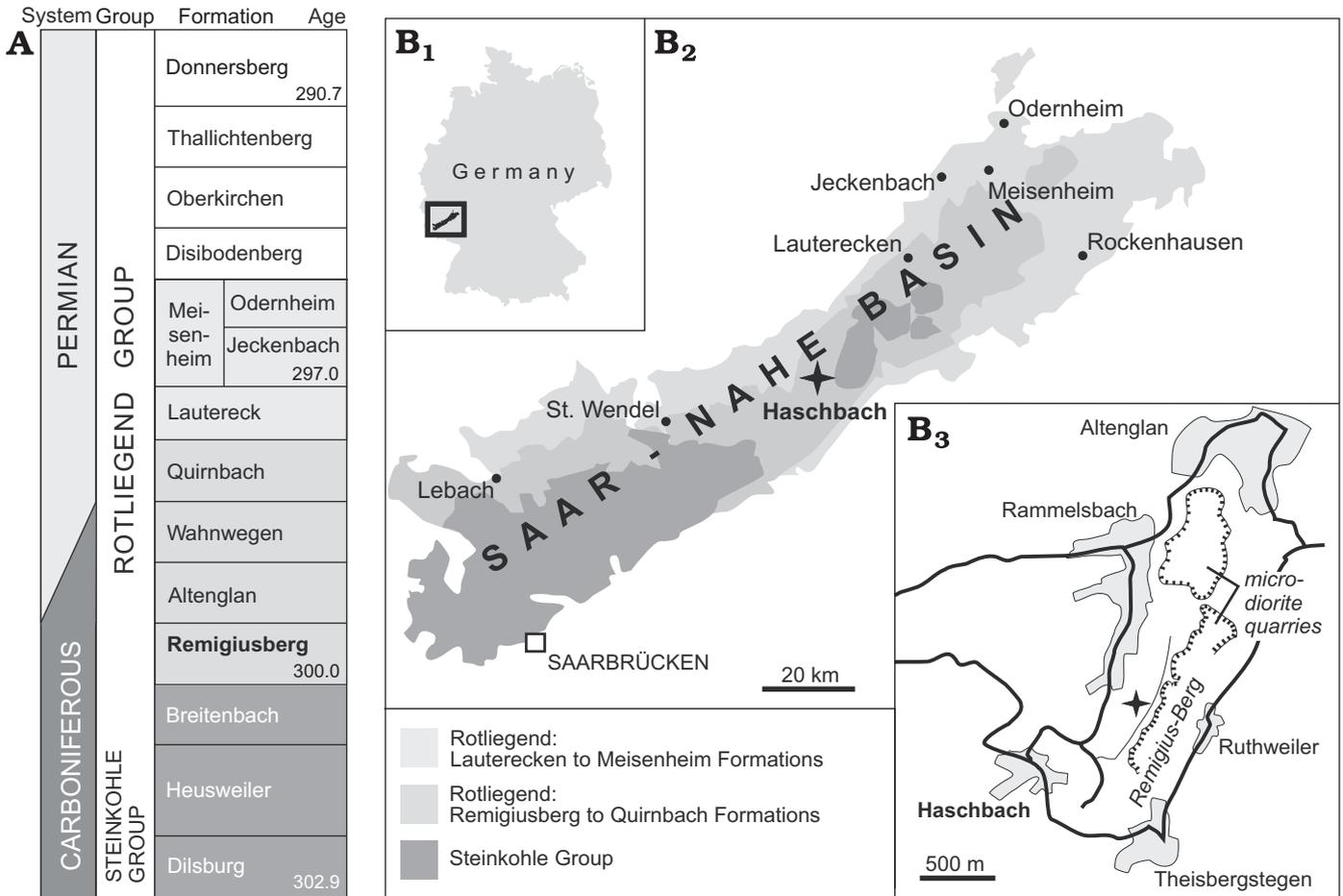


Fig. 1. Geological setting of the locality. **A**. Stratigraphic framework of the Rotliegend in the Saar Nahe Basin. **B**. Location of Saar-Nahe Basin (**B<sub>1</sub>**), geological map of the basin (**B<sub>2</sub>**), and location of the Remigiusberg quarry (**B<sub>3</sub>**). Lithostratigraphy follows Schindler (2007); isotopic ages after Burger et al. (1997), Königler et al. (2002), and Lippolt and Hess (1989); position of the Permo-Carboniferous boundary ( $299.0 \pm 0.8$  Ma) is based on Ogg et al. (2008).

not represent a natural group, they are commonly referred to as non-therapsid or pelycosaur-grade synapsids. This assemblage includes a number of characteristic and well-defined clades, whose inter- and intrarelationships are comparably well resolved and stable (e.g., Reisz 1986; Reisz et al. 1992a, 2009; Laurin 1993; Berman et al. 1995; Modesto 1995; Sidor and Hopson 1998; Maddin et al. 2008; Botha-Brink and Modesto 2009). These clades include Caseasauria (Caseidae and Eothyrididae) as the sister clade of all other synapsids, the Eupelycosauria, comprising Varanopidae, Ophiacodontidae, Edaphosauridae, and Sphenacodontia. Sphenacodontia consist of a number of mainly European stem taxa such as *Haptodus*, as well as Sphenacodontidae, including Sphenacodontidae and Therapsida.

As sister taxon of Therapsida, sphenacodontids are central to our understanding of therapsid origins and the acquisition of mammalian characters within synapsids. Moreover, the moderately to large-sized sphenacodontids from the Late Carboniferous and Early Permian represented the dominant terrestrial predators of their time and are thus particularly important for understanding the evolution of terrestrial ecosystems. A number of genera are currently recognised within Sphenacodon-

tidae. The four best-known genera, *Dimetrodon*, *Sphenacodon*, *Secodontosaurus*, and *Ctenospondylus*, are based on several well-preserved skulls and skeletons and are mainly known from North America; the only exceptions being *Dimetrodon teutonius* from Thuringia, Germany (Berman et al. 2001, 2004), and a possible occurrence of *Sphenacodon*, previously "*Oxyodon*" *britannicus* (see Huene 1908; Paton 1974), from the English midlands (but see Eberth 1985). In addition, the poorly known *Bathygnathus* from Prince Edward Island, Canada, *Macromerion* from Kounová, Czech Republic, and *Neosaurus* from Moisey, France, are based mainly on isolated maxillae (e.g., Leidy 1854; Fritsch 1889; Nopcsa 1923).

Here we report the first amniote from the Saar-Nahe Basin, consisting of a diagnostic anterior portion of a right mandible with 11 teeth and one empty alveolus. It can be safely referred to Sphenacodontidae, whose presence in that basin is otherwise indicated only by the ichnotaxon *Dimetropus*, which occurs in several horizons of the Lower Rotliegend (Voigt 2007). The new mandible originates from the very base of the Rotliegend, which falls into the latest Carboniferous (see Fig. 1 and citations therein). As such it is the oldest amniote record from Germany, and among European

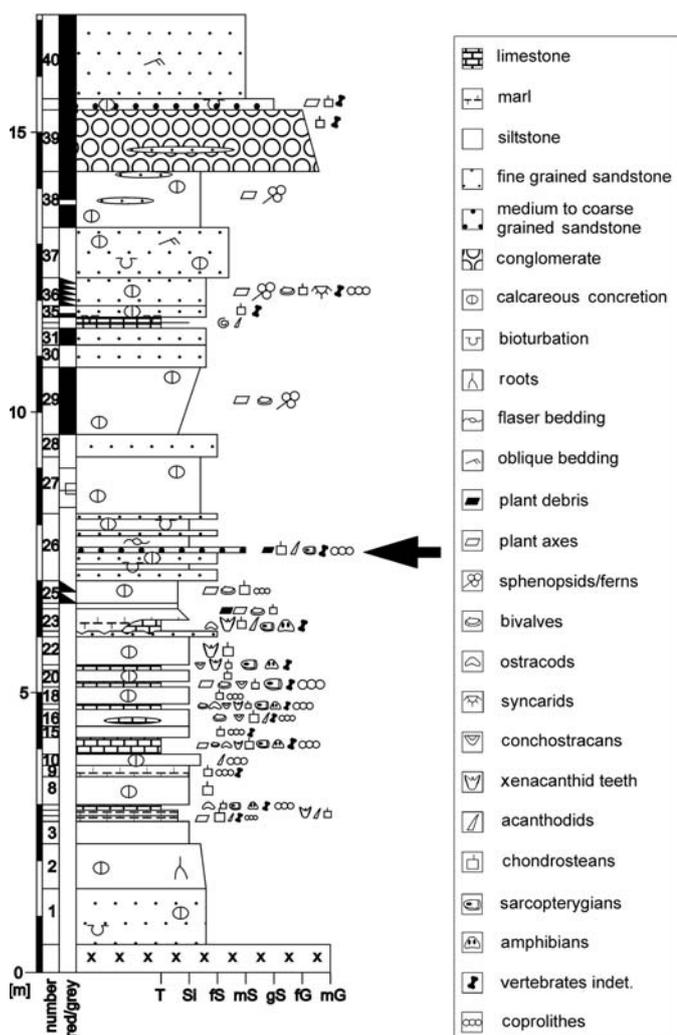


Fig. 2. Lithological column of the Remigiusberg quarry, arrow marks the horizon (layer 26) of the holotype of *Cryptovenator hirschbergeri*.

sphenacodontids it is the second oldest in stratigraphic age to *Macromerion schwarzenbergii* from the Stephanian B (Gzhelian) of Kounová, Czech Republic (Fritsch 1889; Romer 1945; see Supplementary Online Material at [http://app.pan.pl/SOM/app56-Frobisch\\_etal\\_SOM.pdf](http://app.pan.pl/SOM/app56-Frobisch_etal_SOM.pdf)).

*Institutional abbreviation.*—LFN, Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany.

## Geological setting

The locality of the new find, an anterior portion of a sphenacodontid mandible (LFN-PW 2008/5599-LS), is at the western rim of the Remigiusberg quarry (49°54'88''N, 7°26'05''E) on the summit of the Remigiusberg mountain range (Fig. 1), about 1 km northeast of Haschbach in Rhineland Palatinate, Germany. LFN-PW 2008/5599-LS originates from a dark, fine grained sandstone of the middle Remigiusberg Formation in layer 26 of the quarry profile (Fig. 2), which forms part of a lac-

ustrine, mixed carbonate-siliciclastic sequence, representing the lower part of Lake Theisbergstegen (Boy and Schindler 2000). The fauna of this lake deposit falls within the climax of the “Remigiusberg invasion”, an ecostratigraphic bio-event described by Boy and Schindler (2000).

Large blocks of these beds (1–3 m in length) were deposited by quarry workers alongside a dirt road paralleling the western cliff of the Remigiusberg quarry (Fig. 1B). The sphenacodontid mandible was found in one of these blocks of calcareous, fine-grained sandstone of gray-blue-green colour with coarse silty lamina. Examination of the same blocks in 2008 yielded fragments of acanthodians and palaeonisciforms. The bones, scales, and teeth have a bright white coloration as a result of contact metamorphism of the sediments with subvolcanic intrusions.

The age of the fine grained sandstone of the middle Remigiusberg Formation is basal Rotliegend, late Gzhelian, latest Carboniferous (Fig. 1). The available radiometric date for this formation is 300.0 Ma ±2.4 Ma (Lippolt and Hess 1989; Burger et al. 1997; Menning et al. 2000; Königer et al. 2002), which agrees with ecostratigraphic evidence for a late Stephanian age (Boy and Schindler 2000). The new find is therefore older than all other sphenacodont material reported from Europe, except for *Macromerion schwarzenbergii* from the Stephanian B Czech locality of Kounová (Romer 1945; see SOM).

## Systematic palaeontology

Synapsida Osborn, 1903

Sphenacodontia Romer and Price, 1940

Sphenacodontidae Williston, 1912

Genus *Cryptovenator* nov.

*Etymology:* *Crypto* from Greek, *kryptos* (hidden, secret); *venator*, from Latin (hunter).

*Type species:* *Cryptovenator hirschbergeri* sp. nov.; see below.

*Diagnosis.*—As for type species.

*Cryptovenator hirschbergeri* sp. nov.

Fig. 3.

*Etymology:* Named after the county commissioner of Kusel, Dr. Winfried Hirschberger, for his untiring support of the Geoskop Umweltmuseum and of the scientific research in the Saar-Nahe Basin.

*Holotype:* LFN-PW 2008/5599-LS, an anterior right mandible fragment exposed in lateral view with 11 teeth and one empty socket (Fig. 3).

*Type locality:* At the western rim of the Remigiusberg quarry (49°54'88''N, 7°26'05''E), about 1 km northeast of Haschbach in Rhineland Palatinate, Germany (Fig. 1).

*Type horizon:* Layer 26 of the Remigiusberg quarry profile (Fig. 2), a dark, fine grained sandstone of the middle Remigiusberg Formation (300.0 Ma ±2.4 Ma), basal Rotliegend, upper Stephanian, late Gzhelian, latest Carboniferous.

*Diagnosis.*—A basal sphenacodontid synapsid autapomorphic in the shortness and robustness of the lower jaw with

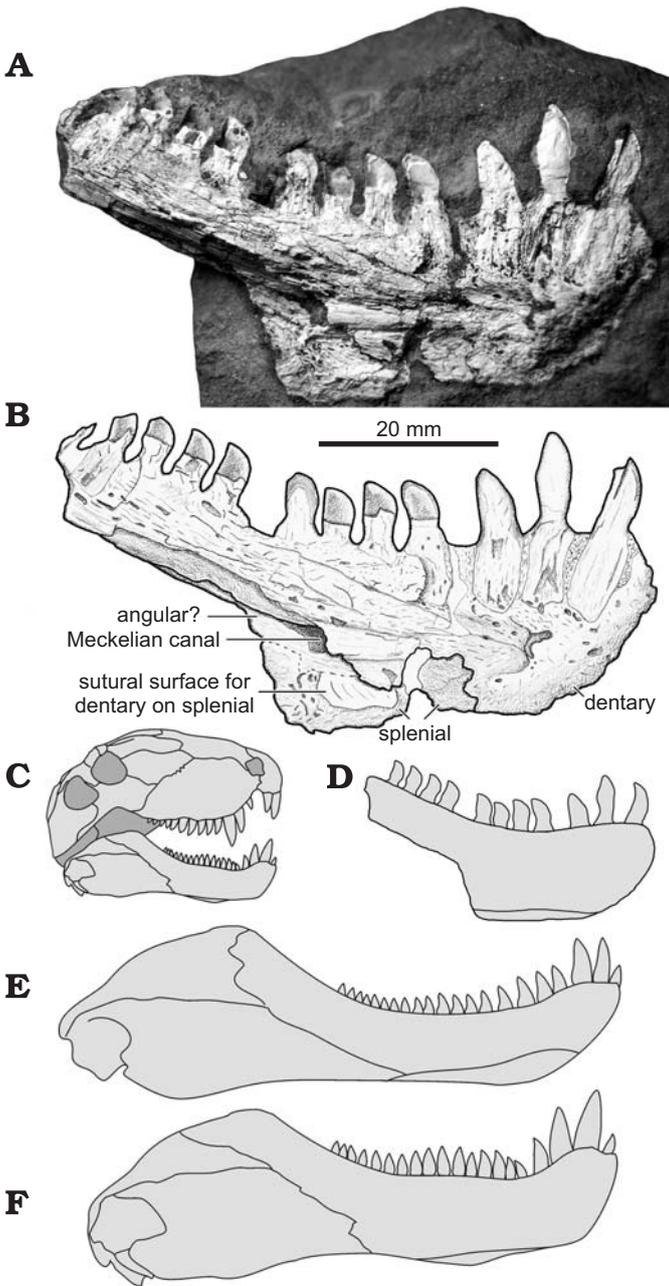


Fig. 3. The holotype of *Cryptovenator hirschbergeri* gen. et sp. nov. (LFN-PW 2008/5599-LS), Remigiussberg Formation (Upper Carboniferous), Rhineland Palatinate, Germany. **A**. Photograph. **B**. interpretative drawing. **C**, **D**. Diagrammatic illustrations of skull of *Dimetrodon grandis* (**C**) and *Cryptovenator hirschbergeri* (**D**). **E**, **F**. Diagrammatic illustrations of isolated mandibles of *Sphenacodon ferocior* (**E**) and *Dimetrodon grandis* (**F**). C, E, F after Romer and Price (1940).

moderate heterodonty, including the absence of a greatly reduced first tooth and only a slight development of the second and third teeth into canines. Shares with *Dimetrodon*, *Sphenacodon*, and *Ctenospondylus*, but not *Secodontosaurus*, enlarged canines and a characteristic teardrop outline of the marginal teeth in lateral view, possession of a deep symphyseal region, and a strongly concave dorsal margin of the dentary.

*Description*.—Only approximately 40–50% of the mandible

is preserved in the holotype of *Cryptovenator hirschbergeri*, including the symphyseal and mid-portion regions, containing 11 teeth and one alveolus. The specimen is partially imbedded in matrix and exposes a longitudinal section of the mandible in lateral view (Fig. 3); the counterslab was not found. The labial sides of the teeth are slightly damaged, the only exception being the enlarged second tooth (canine), whereas the general outline is well preserved in almost all the teeth. An unusual feature of the mandible is not only the depth of the symphyseal region (more than two times the length of one canine and a feature characteristic of sphenacodontids), but also the fact that the depth of the mandible continues posteriorly to its broken margin. At the level of the fourth postcanine the mandible is almost as deep as at the symphysis. This morphology is similar to the condition in *Dimetrodon grandis* and *D. limbatus* (Romer and Price 1940), although it is even more pronounced in *Cryptovenator*. This suggests that the present taxon had a more robust mandible than all other known sphenacodontids, which clearly represents an autapomorphy. The preserved mid-portion of the mandible is markedly concave dorsally, a feature shared by all sphenacodontids, being most pronounced in the smaller species of the genus *Dimetrodon*, such as *Dimetrodon natalis* and *D. milleri*, as well as in *Sphenacodon* (Romer and Price 1940; Eberth 1985).

The preserved anterior portion of the mandible is mainly composed of the dentary. However, as a result of its preservation as longitudinal section, the holotype mandible of *Cryptovenator* also exposes parts of the splenial and angular bones (Fig. 3B). The splenial makes up the posteroventral edge of the preserved mandible and exhibits on its lateral side an obvious facet for the dentary, which is broken off in this area. The exposure of the splenial at a level farther ventral than the dentary suggests that the splenial was likely visible near the symphysis in lateral view. The angular is positioned between the splenial ventrally and dentary dorsally, forming the medial and ventral walls of the Meckelian canal, comparable to the condition in *Dimetrodon* (Romer and Price 1940: fig. 14). The broken posterodorsal edge of the mandible exhibits an additional element in cross-section on the medial side of the dentary that likely represents the anterior coracoid. The Meckelian canal is well exposed as a sediment-filled hole in the centre of the mandible, being bordered by the angular medially and ventrally and the dentary dorsally and laterally. In addition, the symphyseal region of the lower jaw is strongly vascularised, as is typical for sphenacodontids (Eberth 1985), being indicated by a large number of foramina and canals that are exposed in the longitudinal section of the anterior part of the dentary (Fig. 3B).

The dentition in the lower jaw of *Cryptovenator* clearly identifies this taxon as sphenacodontid synapsid, based on two main features: (i) the presence of enlarged canines, specifically the second and third dentary teeth, and (ii) the teardrop outline of the marginal teeth in lateral view. Nonetheless, *Cryptovenator* is autapomorphic in the development of moderate heterodonty only. This is expressed by the absence of a greatly reduced first tooth and only a slight development of the



sistent with those of the previous analyses (Reisz et al. 1992a; Laurin 1993; Kissel and Reisz 2004). *Haptodus* (based on *Haptodus garnettensis* and not the type species *H. baylei*) represents the most basal sphenacodontian and *Cutleria* represents the sister taxon of Sphenacodontoidea. In contrast to previous analysis, the relationships of the haptodontine-grade sphenacodontians *Palaeohatteria*, *Pantelosaurus* and *Ianthodon* are not resolved; instead they form a polytomy with *Cutleria* + Sphenacodontoidea. The analysis recovers a monophyletic Sphenacodontidae as the sister taxon of therapsids, exemplified by *Biarmosuchus* and *Dinocephalia*. However, the position of *Secodontosaurus* at the base of Sphenacodontidae is novel. The new taxon from the Saar-Nahe Basin, *Cryptovenator hirschbergeri*, represents the progressively more derived taxon with a sister-taxon relationship to the well-supported but unresolved monophylum that includes *Sphenacodon*, *Ctenospondylus*, and *Dimetrodon*.

## Discussion and conclusions

*Cryptovenator hirschbergeri* can be unequivocally referred to the synapsid family Sphenacodontidae Williston, 1912, on the basis of its enlarged canines, characteristic teardrop outline of the marginal teeth in lateral view, possession of a deep symphyseal region, and the pronounced upward curvature of dorsal margin of the dentary (Fig. 3). These features are shared only with the advanced sphenacodontid genera *Dimetrodon*, *Sphenacodon*, and *Ctenospondylus*, but notably not *Secodontosaurus* or the more basal haptodontine-grade sphenacodontians. Moreover, *Cryptovenator* is autapomorphic in the extreme shortness and robustness of the lower jaw and the development of moderate heterodonty only. This includes the absence of a greatly reduced first tooth and only a slight caniniform development of the second and third teeth. The heterodonty is much more pronounced in *Sphenacodon*, *Ctenospondylus*, and *Dimetrodon*, whereas it is absent in *Secodontosaurus*. In addition, the phylogenetic analysis of sphenacodontian synapsids (Fig. 4) indicates that *Cryptovenator* represents a basal member of the Sphenacodontidae, being less derived than most primarily Permian taxa.

The phylogenetic position of *Secodontosaurus* at the base of Sphenacodontidae, as suggested by the current phylogenetic analysis, warrants further discussion. Previously, material of *Secodontosaurus* has variously been identified as belonging to an ophiacodontid and, more recently, to a sphenacodontian synapsid (Cope 1880; Case 1907; Williston 1916; Romer 1936; Romer and Price 1940; Reisz et al. 1992a, b). Romer and Price (1940) further discussed the phylogenetic relationships of *Secodontosaurus* within Sphenacodontia, offering two alternative hypotheses: (i) *Secodontosaurus* as an advanced sphenacodontid; or (ii) *Secodontosaurus* as a basal haptodontine-grade sphenacodontian. They favoured the second hypothesis, whereas Reisz et al.'s (1992a) cladistic analysis of sphenacodontids supported the first hypothesis and a sister-taxon relationship of *Secodontosaurus* with *Dimetrodon*,

mainly supported by characters of the neural spines. All of those characters are also included in the present phylogenetic analysis. However, whereas the resulting phylogenetic position of *Secodontosaurus* at the base of sphenacodontids represents a novel hypothesis of sphenacodontid relationships, the decay and bootstrap values indicated that it is robust (Fig. 4). The topology within Sphenacodontidae is particularly well supported when *Cryptovenator* is excluded from the analysis (Fig. 4B). A monophyletic Sphenacodontinae (sensu Romer and Price 1940; contra Reisz et al. 1992a) to the exclusion of *Secodontosaurus* (and possibly *Cryptovenator*) is supported by the following characters: (1) orbital process of frontal extends far laterally; (2) extensive postorbital-squamosal contact; (3) supratemporal-postorbital contact; (4) small contribution of lacrimal to orbit; (5) narrow, blade-like paroccipital process; (6) one to three maxillary precaniniform teeth; (7) strongly convex maxilla ventral margin; (8) dorsoventrally deepened symphyseal region of the dentary (also present in *Cryptovenator*); (9) teardrop shaped marginal teeth (also present in *Cryptovenator*); (10) greatly enlarged second dentary tooth. Nonetheless, *Secodontosaurus* clearly represents a sphenacodontid synapsid and *Cryptovenator* seems to be intermediate between the former taxon and a monophyletic Sphenacodontinae that includes *Sphenacodon*, *Ctenospondylus*, and *Dimetrodon*.

The discovery of a sphenacodontid in the Remigiussberg Formation of the Saar-Nahe Basin is unexpected because this formation has so far not yielded any remains of larger tetrapods or their tracks, whereas large quantities of tetrapods are found only in much higher stratigraphic levels, predominantly in the Lauterecken and Meisenheim formations (Boy 1987; Schindler 2007). However, tracks of synapsids are known from beds above the Remigiussberg Formation (Voigt 2007), and judging from ichnological evidence, synapsids must have been much more widespread and long-ranging than suggested by this single skeletal find. Synapsid tracks have a long stratigraphic range in the Saar-Nahe Basin, occurring throughout the Altenglan and Standenbühl formations and spanning a time interval of at least 10 Ma (Voigt 2007).

*Cryptovenator hirschbergeri* is not only one of the oldest synapsids, but also represents the oldest skeletal remain of an amniote from Germany. With the exception of *Macromerion schwarzenbergii* from the Stephanian B (Gzhelian) of Kounová (a maxilla very similar to *Dimetrodon*, see Romer 1945), all other European sphenacodontids are substantially younger than *Cryptovenator*, occurring in the Early Permian (see SOM). They either date to the Asselian–Sakmarian (Autun, Döhlen, and Silesian material) or Artinskian (Tambach Formation) (e.g., German Stratigraphic Commission 2002; Schneider and Werneburg 2006). Even the more primitive haptodontine-grade sphenacodontians, such as *Haptodus*, *Palaeohatteria*, and *Pantelosaurus*, make their first occurrence only slightly above the stratigraphic levels of the Kounová and Remigiussberg finds (Kissel and Reisz 2004).

Sphenacodontians were the largest terrestrial predators of their time, ranging in body length between 60 cm (*Haptodus*

*garnettensis*, *Dimetrodon teutonius*) and 320 cm (*Dimetrodon grandis*). The Remigiusberg specimen (*Cryptovenator*) pertains to a relatively small animal (estimated 100 cm), which is consistent with the size of some *Dimetrodon* tracks, although other tracks of up to 20 cm pedal length indicate that much larger sphenacodontians must have been present in the Saar-Nahe Basin (see Voigt 2007). Nonetheless, *Cryptovenator* predates the record of sphenacodontid tracks in the Saar-Nahe Basin, as the oldest occurrence of *Dimetrodon* tracks is in the slightly younger Wahnwegen Formation (Voigt 2007).

The palaeoenvironment of Lake Theisbergstegen was analysed by Boy and Schindler (2000). The biofacies of this deposit includes root horizons and mud cracks, and is characterized by a rapid lateral change of beds, which suggests shallow water conditions. The discovery of a terrestrial amniote is therefore not surprising, although certainly a rare event. Vertebrates from the same beds include only aquatic taxa, among them acanthodians and small, smooth-scaled palaeonisciforms. In general, the lake deposits of the Remigiusberg time interval were small and shallow, but rich in species (Boy and Schindler 2000; Schindler 2007). It is probable that such small lake deposits are more likely to bear terrestrial tetrapods, which is one type of deposit to be focused on in the further search for amniote remains.

The Late Carboniferous occurrence of sphenacodontids, the most derived pelycosaur-grade synapsids, once more emphasises that the major phylogenetic diversification of early amniotes took place well before the Permo-Carboniferous transition. However, as a result of the comparatively poor fossil record of Carboniferous amniotes, it remains unclear if this diversification event proceeded relatively fast within only few million years, or if it occurred over a longer period of time, thereby extending well into the earlier Carboniferous.

## Acknowledgements

We are very grateful to Rudolf Bold (Rammelsbach, Germany), the collector of the specimen. We wish to thank the General Department of Cultural Heritage Rhineland Palatinate, Department Archaeology, Section Geological History of the Earth, for technical and financial support. Jürgen A. Boy (Johannes Gutenberg Universität Mainz, Germany) kindly provided field data of the Remigiusberg quarry. Comments made by two anonymous reviewers as well as Jörg Schneider (Technische Universität Bergakademie Freiberg, Germany) and the editor Richard Cifelli (University of Oklahoma, Norman, USA) greatly helped to improve this work. This study was financially supported by the Deutsche Forschungsgemeinschaft (FR 2457/3-1, to JF; Mu 1760/2-3, to JM).

## References

Berman, D.S., Henrici, A.C., Sumida, S.S., and Martens, T. 2004. New materials of *Dimetrodon teutonius* (Synapsida: Sphenacodontidae) from the Lower Permian of Germany. *Annals of Carnegie Museum* 73: 48–56.  
 Berman, D.S., Reisz, R.R., Bolt, J.R., and Scott, D. 1995. The cranial anatomy and relationships of the synapsid *Varanosaurus* (Eupelycosauria,

Ophiacodontidae) from the Early Permian of Texas and Oklahoma. *Annals of Carnegie Museum* 64: 99–133.  
 Berman, D.S., Reisz, R.R., Martens, T., and Henrici, A.C. 2001. A new species of *Dimetrodon* (Synapsida: Sphenacodontidae) from the Lower Permian of Germany records first occurrence of genus outside of North America. *Canadian Journal of Earth Sciences* 38: 803–812. [CrossRef]  
 Botha-Brink, J. and Modesto, S.P. 2009. Anatomy and relationships of the Middle Permian varanopid *Heleosaurus scholtzi* based on a social aggregation from the Karoo Basin of South Africa. *Journal of Vertebrate Paleontology* 29: 389–400. [CrossRef]  
 Boy, J.A. 1977. Typen und Genese jungpaläozoischer Tetrapoden-Lagerstätten. *Palaeontographica A* 156: 111–167.  
 Boy, J.A. 1987. Die Tetrapoden-Lokalitäten des saarpfälzischen Rotliegenden (?Ober-Karbon–Unter-Perm; SW-Deutschland) und die Biostratigraphie der Rotliegend-Tetrapoden. *Mainzer geowissenschaftliche Mitteilungen* 16: 31–65.  
 Boy, J.A. 2003. Paläoökologische Rekonstruktion von Wirbeltieren: Möglichkeiten und Grenzen. *Paläontologische Zeitschrift* 77: 123–152.  
 Boy, J.A. 2007. Als die Saurier noch klein waren: Tetrapoden im Permo-karbon. In: T. Schindler and U.H.J. Heidtke (eds.), *Kohlesümpfe, Seen und Halbwüsten*, 256–286. Pollichia Sonderveröffentlichungen 10, Bad Dürkheim.  
 Boy, J.A. and Schindler, T. 2000. Ökostratigraphische Bioevents im Grenzbereich Stephanium/Autunium (höchstes Karbon) des Saar-Nahe-Beckens (SW-Deutschland) und benachbarter Gebiete. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 216: 89–152.  
 Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795–803. [CrossRef]  
 Burger, K., Hess, J.C., and Lippolt, H.J. 1997. Tephrochronologie mit Karolin-Kohlensteinen: Mittel zur Korrelation paralischer und limnischer Ablagerungen des Oberkarbons. *Geologisches Jahrbuch A* 147: 3–39.  
 Case, E.C. 1907. Revision of the Pelycosauria of North America. *Publications of the Carnegie Institution of Washington* 55: 1–176.  
 Cope, E.D. 1880. Second contribution to the history of the Vertebrata of the Permian formation of Texas. *Proceedings of the American Philosophical Society* 19: 38–58.  
 Credner, H. 1888. Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. VII Theil: *Palaeohatteria longicaudata* Cred. *Zeitschrift der deutschen geologischen Gesellschaft* 40: 490–558.  
 Currie, P.J. 1979. The osteology of haptodontine sphenacodonts (Reptilia: Pelycosauria). *Palaeontographica Abteilung A* 163: 130–168.  
 Eberth, D.A. 1985. The skull of *Sphenacodon ferocior*, and comparison with other sphenacodontines (Reptilia: Pelycosauria). *New Mexico Bureau of Mines and Mineral Resources Circular* 190: 5–39.  
 Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791. [CrossRef]  
 Fichter, J. 1983. Tetrapodenfährten aus dem saarpfälzischen Rotliegenden (Ober-Karbon–Unter-Perm; SW-Deutschland) II: Fährten der Gattungen *Foliipes*, *Varanops*, *Ichniotherium*, *Dimetrodon*, *Palmichnus*, *Phalangichnus*, cf. *Chelichnus*, *Ichniotherium*, cf. *Laoorus* und *Anhomoichnium*. *Mainzer naturwissenschaftliches Archiv* 21: 125–186.  
 Fritsch, A. 1889. *Fauna der Gaskohle und Permformation Böhmens*. 192 pp. Published by the author, Prague.  
 Gaudry, A. 1886. Sur un nouveau genre de reptile trouvé dans le Permien d'Autun. *Bulletin de la Société géologique de France* 14: 430–433.  
 German Stratigraphic Commission 2002. *Stratigraphic Table of Germany 2002*. Stein, Potsdam.  
 Haubold, H. 1973. Die Tetrapodenfährten aus dem Perm Europas. *Freiberger Forschungshefte C* 285: 5–55.  
 Huene, F. von 1908. Neue und verkannte Pelycosaurier-Reste aus Europa. *Centralblatt für Mineralogie, Geologie und Paläontologie* 14: 431–434.  
 Huene, F. von 1925. Ein neuer Pelycosaurier aus der unteren Permformation Sachsens. *Geologische und paläontologische Abhandlungen* 14: 215–264.  
 Kemp, T.S. 1982. *Mammal-like Reptiles and the Origin of Mammals*. 363 pp. Academic Press, London.

- Kemp, T.S. 2005. *The Origin and Evolution of Mammals*. 331 pp. Oxford University Press, Oxford.
- Kissel, R.A. and Reisz, R.R. 2004. Synapsid fauna of the Upper Pennsylvanian Rock Lake Shale near Garnett, Kansas and the diversity pattern of early amniotes. In: G. Arratia, M.V.H. Wilson, and R. Cloutier (eds.), *Recent Advances in the Origin and Early Radiation of Vertebrates*, 409–428. Pfeil Verlag, München.
- Königer, S., Lorenz, V., Stollhofen, H., and Armstrong, R.A. 2002. Origin, age and stratigraphic significance of distal fallout ash tuffs from the Carboniferous–Permian continental Saar-Nahe Basin (SW Germany). *International Journal of Earth Sciences (Geologische Rundschau)* 91: 341–356. [CrossRef]
- Laurin, M. 1993. Anatomy and relationships of *Haptodus garnettensis*, a Pennsylvanian synapsid from Kansas. *Journal of Vertebrate Paleontology* 13: 200–229. [CrossRef]
- Leidy, J. 1854. On *Bathynathus borealis*, and extinct saurian of the New Red Sandstone of Prince Edward's Island. *Journal of the Philadelphia Academy of Natural Sciences 2nd series* 2: 327–330.
- Lippolt, H.J. and Hess, J.C. 1989. Isotopic evidence for the stratigraphic position of the Saar-nahe-Rotliegende volcanism. III. Synthesis of results and geological implications. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1989 (9): 553–559.
- Maddin, H.C., Sidor, C.A., and Reisz, R.R. 2008. Cranial anatomy of *Ennatosaurus tecton* (Synapsida : Caseidae) from the middle Permian of Russia and the evolutionary relationships of Caseidae. *Journal of Vertebrate Paleontology* 28: 160–180. [CrossRef]
- Menning, M., Weyer, D., Drozdowski, G., van Amerom, H.W.J., and Wendt, I. 2000. A Carboniferous time scale 2000: discussion and use of geological parameters as time indicators from central and western Europe. *Geologisches Jahrbuch A* 156: 3–44.
- Modesto, S.P. 1995. The skull of the herbivorous synapsid *Edaphosaurus boanerges* from the Lower Permian of Texas. *Palaeontology* 38: 213–239.
- Nopcsa, F. 1923. *Die Familien der Reptilien*. 210 pp. Verlag von Gebrüder Borntraeger, Berlin.
- Ogg, J. G., Ogg, G., and Gradstein, F.M., eds. 2008. *The Concise Geologic Time Scale*. Cambridge University Press, Cambridge.
- Olson, E.C. 1966. Community evolution and the origin of mammals. *Ecology* 47 (2): 291–302. [CrossRef]
- Osborn, H.F. 1903. On the primary division of the Reptilia into two sub-classes Synapsida and Diapsida. *Science* 17: 275–276. [CrossRef]
- Paton, R.L. 1974. Lower Permian pelycosaurs from the English midlands. *Palaeontology* 17: 541–552.
- Reisz, R.R. 1986. *Pelycosauria*. 102 pp. G. Fischer, Stuttgart.
- Reisz, R.R., Berman, D.S., and Scott, D. 1992a. The cranial anatomy and relationships of *Secodontosaurus*, an unusual mammal-like reptile (Synapsida: Sphenacodontidae) from the early Permian of Texas. *Zoological Journal of the Linnean Society* 104: 127–184. [CrossRef]
- Reisz, R.R., Godfrey, S.J., and Scott, D. 2009. *Eothyris* and *Oedaleops*: do these early Permian synapsids from Texas and New Mexico form a clade? *Journal of Vertebrate Paleontology* 29: 39–47. [CrossRef]
- Reisz, R.R., Scott, D., and van Bendegem, J. 1992b. Atlas-axis complex of *Secodontosaurus*, a sphenacodontid mammal-like reptile (Eupelycosauria, Synapsida) from the Lower Permian of Texas. *Canadian Journal of Earth Sciences* 29: 596–600.
- Romer, A.S. 1936. Studies on American Permo-Carboniferous tetrapods. *Problems of Paleontology, USSR* 1: 85–93.
- Romer, A.S. 1945. The late Carboniferous vertebrate fauna of Kounova (Bohemia) compared with that of the Texas redbeds. *American Journal of Science* 243: 417–442. [CrossRef]
- Romer, A.S. and Price, L.I. 1940. Review of the Pelycosauria. *Geological Society of America Special Paper* 28: 1–538.
- Schindler, T. 2007. Geologie, Stratigraphie und Genese des permokarbonischen Saar-Nahe Beckens. In: T. Schindler and U.H.J. Heidtke (eds.), *Kohlesümpfe, Seen und Halbwüsten*, 4–37. Pollichia Sonderveröffentlichungen 10, Bad Dürkheim.
- Schindler, T. and Heidtke, U.H.J. (eds.) 2007. *Kohlesümpfe, Seen und Halbwüsten*. 280 pp. Pollichia Sonderveröffentlichungen 10, Bad Dürkheim.
- Schneider, J.W. and Werneburg, R. 2006. Insect biostratigraphy of the Euramerican continental Late Pennsylvanian and Early Permian. In: S.G. Lucas, G. Cassinis, and J.W. Schneider (eds.), *Non-marine Permian Biostratigraphy and Biochronology*. *Geological Society of London, Special Publications* 265: 325–336.
- Schoch, R.R. 2009. Evolution of life cycles in early amphibians. *Annual Review of Earth and Planetary Sciences* 37: 135–162. [CrossRef]
- Schroeder, H. 1905. *Datheosaurus macrourus* nov. gen. nov. sp. aus dem Rotliegenden von Neurode. *Jahrbuch der königlich preußischen geologischen Landesanstalt und Bergakademie* 25: 282–294.
- Sidor, C.A. 2003. Evolutionary trends and the origin of the mammalian lower jaw. *Paleobiology* 29: 605–640. [CrossRef]
- Sidor, C.A. and Hopson, J.A. 1998. Ghost lineages and “mammalness”: assessing the temporal pattern of character acquisition in the Synapsida. *Paleobiology* 24: 254–273.
- Swofford, D.L. 2001. *PAUP\*: phylogenetic analysis using parsimony (\*and other methods)*. Sinauer Associates, Sunderland, MA.
- Voigt, S. 2007. Auf den Spuren der Saurier: Die Tetrapodenfahrten aus dem Oberkarbon und Unterperm des Saar-Nahe-Beckens. In: T. Schindler and U.H.J. Heidtke (eds.), *Kohlesümpfe, Seen und Halbwüsten*, 288–303. Pollichia Sonderveröffentlichungen 10, Bad Dürkheim.
- Werneburg, R. and Schneider, J.W. 2006. Amphibian biostratigraphy of the European Permo-Carboniferous. In: S.G. Lucas, G. Cassinis, and J.W. Schneider (eds.), *Non-marine Permian Biostratigraphy and Biochronology*. *Geological Society of London, Special Publications* 265: 201–215.
- Williston, S.W. 1912. Primitive reptiles. A review. *Journal of Morphology* 23 (4): 637–666. [CrossRef]
- Williston, S.W. 1916. The osteology of some American Permian vertebrates, II. *Contribution from Walker Museum* 1: 165–192.